

Frontispiece.—Transverse section of secondary wood of *Ulmus americana*. $\times 50$.
(Courtesy, U. S. Forest Products Laboratory.)

"The Staple of the Stuff is so exquisitely fine, that no Silk-worm is able to draw anything near so fine a Thread. So that one who walks about with the meanest Stick, holds a piece of Natures Handicraft, which far surpasses the most elaborate Woof or Needle-Work in the World."—Nehemiah Grew.

AN INTRODUCTION TO PLANT ANATOMY

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PREFACE

In presenting this book the authors hope to fill a need for a textbook in plant anatomy of a type at present not available—a need which they, as teachers in this field, have keenly felt. Not only, however, in their opinion, is there need for a book for class study and guidance, but also for one which shall serve as a reference text for workers in fields of applied botany, and for teachers and students in other fields of pure botany. A double purpose, therefore, has been kept in mind in the preparation of the book. In the treatment of the subject matter, however, emphasis has been placed on adaptability to classroom use from the standpoint of the student beginning anatomical study. Thus, the book is, first of all, a textbook in the elements of plant anatomy—an introduction to the field. It presupposes an acquaintance only with the fundamental structure and activities of plants—an acquaintance such as is ordinarily obtained from a first course in botany.

Though the book is thus introductory in nature, it is believed to embody a fairly comprehensive treatment of the fundamental facts and aspects of anatomy—to be, in fact, so inclusive as to provide a working basis for independent study. Yet it does not lay claim to the exposition, in detail, of the known facts and the theories concerning any structural features. So great is the number of recorded facts, and so confused is the terminology of anatomy, that a treatise approaching completeness in the presentation thereof would not be usable as a textbook. Further, the anatomy of vascular plants, especially that of the angiosperms is, in detail and in some broader features, still largely unknown. It is thus obviously impossible to present data covering the facts and structural features which will be met by the student in later work. It is, further, the firm opinion of the authors that the student of anatomy should not learn facts primarily, but should be taught self-reliance in the study of plant structure through training in power of observation and interpretation. Therefore, the book is not a compendium of facts.

Training which results in independence in the study of anatomy is, of course, secured only by laboratory practice. On such practice the authors believe emphasis must be placed, and not on lectures, text study, nor, in the beginning, on reading. For laboratory teaching the present book should provide a background of facts, terms, history, etc.; it may, indeed, be used, in part, as a laboratory guide. The sequence of subjects adopted is that which in the experience of the authors has been

found most satisfactory in laboratory work. Such material as is specifically mentioned, or is used for illustration, suggests only in a general way the range and the amount of material that may be used in a first course in plant anatomy. It is not necessary, nor is it even desirable, that the same plants be used in the classroom. Any available material may be used, and, by comparison with the descriptions and illustrations of the text, the teaching can be made more effective. The authors in their own classes use considerable material, sufficient to cover so far as possible the range and type of variation in each structure. An acquaintance with variation is thus acquired by the student, and a power of interpretation is given by practice with many examples, so that he is enabled thereafter to interpret wholly new material.

As a reference book, the synoptical treatment of the more important facts, usage of terms, present status of opinion, etc. should render the book generally useful. More detailed information may be obtained, of course, from the larger reference works, though in many cases it is only to be found in papers and articles of limited scope. A certain small amount of material embodied in the book represents the result of unpublished research and observation on the part of the authors, or represents their personal opinions.

Except for an occasional mention of lower forms, the structure of vascular plants only is considered, since the histological structure of the thallophytes is usually not complex. In cases where it is, the method of study and the terms applied to cells and tissues in higher plants may generally be used. In the selection of forms for illustration there have been chosen, so far as available material has permitted, well-known or economically important plants.

The viewpoint of the treatment is fundamentally that of descriptive morphology, that is, of existent form and structure. Physiological anatomy regards form but little; and an understanding of form and of structural relationship must precede all valuable anatomical study. The physiological aspects and the practical bearing of the subject matter are discussed briefly, and incidentally to the general treatment. Comparative morphology is made use of whenever an understanding of phylogenetic development helps to make structural complexity clear. A textbook written on the basis of descriptive morphology the authors believe to be most generally useful. For students going beyond the introductory steps in anatomy, however—either into the various fields of applied subjects, such as pathology and horticulture, or into any field of the pure science—a complete understanding of morphological modification and variation can be obtained only through the consideration of the phylogenetic history of the structure in question.

The book does not pretend to present the historical development of our knowledge of the field, or of any phase or part thereof; nor are the contributions of prominent students brought out as the work of individuals. The present status of knowledge and opinion is made the first aspect of treatment; secondarily, other viewpoints are considered. Chapter XV, however, outlines the history of the subject, and deals briefly with the contributions of some of the earlier prominent students of anatomy. This historical sketch is placed at the end of the book, since the beginning student may best make use of it only when he has acquired an understanding of the subject matter.

Owing to the state of confusion which exists in the terminology of anatomy, it has in many cases been necessary to evaluate the different uses of terms. For use in the book, those terms have been accepted which seem best on a basis first of morphological usefulness and secondly, of priority; in a few instances the history and the use of a term are briefly discussed.

Since the book is primarily an elementary text and not a text for research reference nor for the use of advanced students, the bibliography has been kept at a minimum. After each chapter there are listed a few of the more recent and more important books and articles—and sometimes those valuable for their own bibliographies—dealing with the subjects discussed in that chapter. By reference to these, students may obtain longer lists. Such a method of citation naturally often excludes the older, "classic" treatments. To the first chapter is appended a list of texts which are generally useful for some or for many phases of the subject. Reference to these texts is not repeated after the various chapters, except in a few cases where the book in question deals particularly with the subject matter of a chapter.

The common names of plants have for the most part been omitted from the text. They may be sought in the index, as such, and also under the generic names with which they are associated.

In present-day botany, the terms "anatomy" and "histology" are often loosely used. To many botanists the study of the internal structure of plants is unfortunately known as histology. This is doubtless due in part to the fact that histology deals with the structure of cells and tissues—internal structure meaning this and little more—and in part to the fact that the grosser internal structures, such as steles and traces, have been consistently neglected in courses in "histology." The study of these features of grosser internal structure, and sometimes of those of external make-up also, have been looked upon as "anatomy." Anatomy, however, deals with the structure of organisms, structure both gross and minute, external and internal. Histology, which deals with the minute structure of organisms, is, therefore, a part of the broader field of anatomy. An understanding of the structure of a plant obviously cannot

be obtained from the study of minute features alone. Thus, a treatment such as is here presented is anatomical rather than histological, and the book is, therefore, a text in Plant Anatomy.

In so far as the treatment in its histological aspects deals with the structure of cells—especially wherever the protoplast is concerned—it enters the field of cytology; and cytology in recent years has become an independent division of biological science. Cytological aspects of anatomy, therefore, need not be considered, and have been omitted from the discussion except in so far as they are essential to histological study. An arbitrary limit has necessarily been set to the description of the cell. The protoplast is very briefly discussed, except for the paragraphs on plasmodesma, plastids, and cell inclusions; nuclear division is omitted since it is ordinarily taught in first courses in botany, and again in greater detail in cytology. The wall, however, which, aside from aspects of origin and early development, is usually considered by cytologists as a histological feature, is more fully treated.

The illustrations have in large part been made directly from the material itself. The explanation of the figures is placed chiefly in the legends. With a few exceptions, the drawings are the work of the authors themselves and of Mrs. Rita Ballard Eames to whom the authors are greatly indebted for invaluable assistance and suggestions. The helpful criticism of their colleagues the authors also desire to acknowledge.

A. J. E.
L. H. M.

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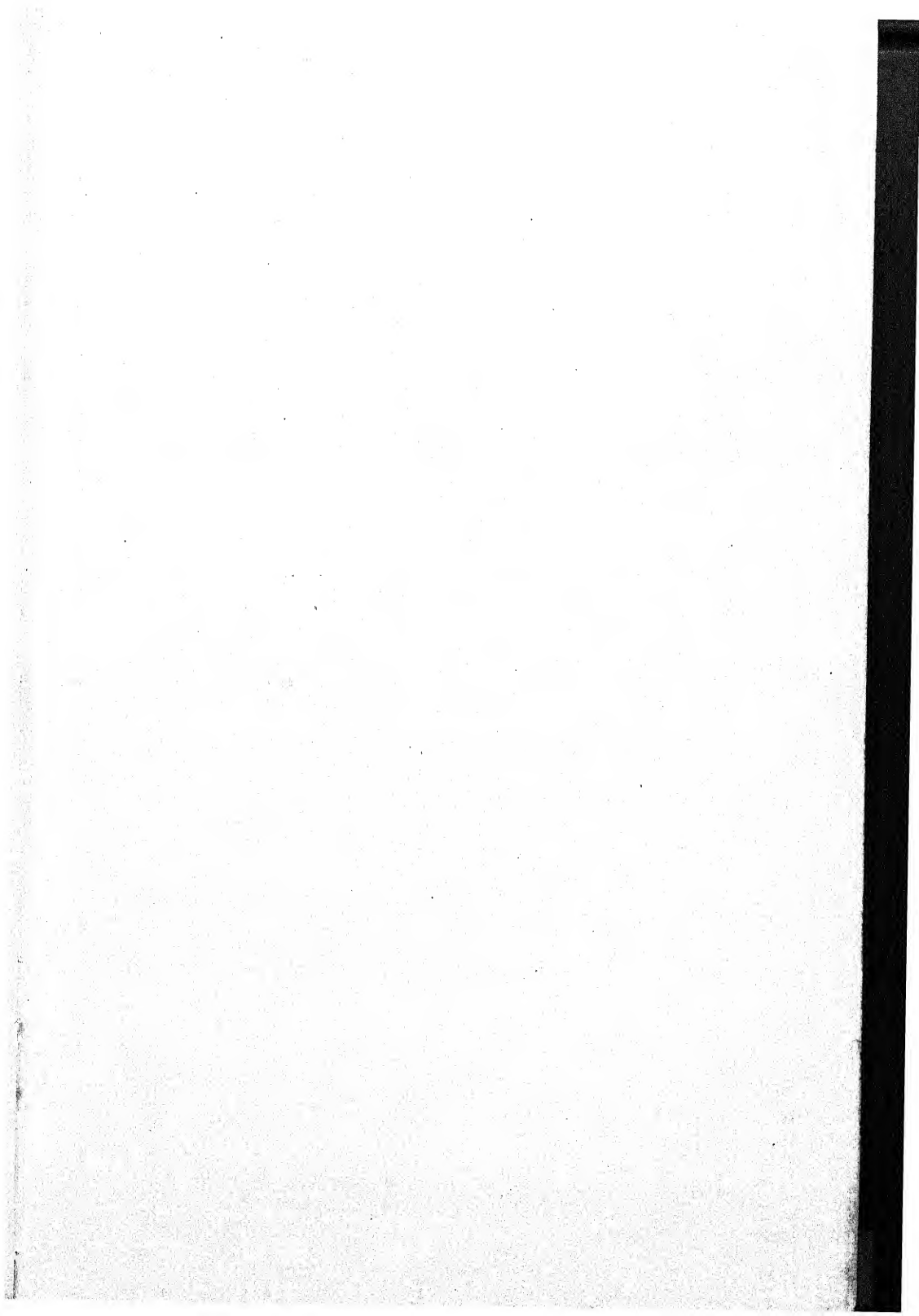
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"I know it will be difficult to make observations of this kind upon the *Organical Parts* of *Plants*, severally. . . . For what we obtain of *Nature*, we must not do it by commanding, but by courting of Her . . . I mean, that where ever Men will go beyond Phansie and Imagination, . . . they must Labour, Hope and Persevere . . . And as the means propounded, are all necessary, so they may, in some measure, prove effectual. How far, I promise not; the Way is long and dark . . . If but little should be effected, yet to design more, can do us no harm: For although a Man shall never be able to hit *Stars* by shooting at them; yet he shall come much nearer to them, than another that throws at *Apples*.—Nehemiah Grew, *The Anatomy of Plants*, 1682.

AN INTRODUCTION TO PLANT ANATOMY

CHAPTER I

GENERAL STRUCTURE OF THE PLANT BODY—AN OUTLINE

Among vascular plants there is very great diversity in size, form, and structure; yet, underlying the variations in form and the complexities in structure in the plant body, there is a simple, uniform, structural plan. The body consists fundamentally of a cylindrical axis which bears lateral appendages. The more or less free branching of the axis and the variety and complexity of the appendages, however, often conceal this simplicity of plan.

Fundamental Parts of the Plant Body.—The axis, though a continuous structure, consists of two parts, different structurally and physiologically, and clearly morphologically distinct: that portion which is normally aerial is known as the *stem*, and that portion which is subterranean is called the *root* (Fig. 1). The appendages are of three ranks. Those into which pass strands of vascular tissue may be said to be of the first rank, and are known as *leaves*. Appendages of this type are characteristic of the stem and do not occur on the root. They are arranged in a definite manner, and bear an intimate structural relation to the skeleton of the axis. The leaf may be looked upon from the standpoint of the present treatment as a lateral expansion of the stem, continuous with it, in the formation of which all fundamental parts of the stem are concerned. Only the outermost layers of the stem, the cortex and the epidermis, are usually present in appendages of the second rank. These are known as *emergences*; the prickles of the rose are a familiar example. In appendages of the third rank, projections of the outermost layer of cells only are present; these form *hairs*. Emergences and hairs occur on both axis and leaves, usually without definite arrangement.

The Axis.—The axis itself consists of a central core with a surrounding, ensheathing layer. This core serves chiefly the important functions of conduction and support; it contains the *vascular tissue* and the larger part of all the supporting and conducting cells of the mature axis. Because of its shape and its position in the axis, this central unit mass is known as the *central cylinder*, or *stele* (Fig. 2). The surrounding layer,

which serves for protection, support, storage, and for other purposes, is the *cortex*; the outermost layer of cells is the *epidermis*.

The Stele.—Primarily, the stele is composed of vascular tissue of two types: that which conducts water and other substances absorbed from the soil, the *xylem*; and that which carries the food (and possibly

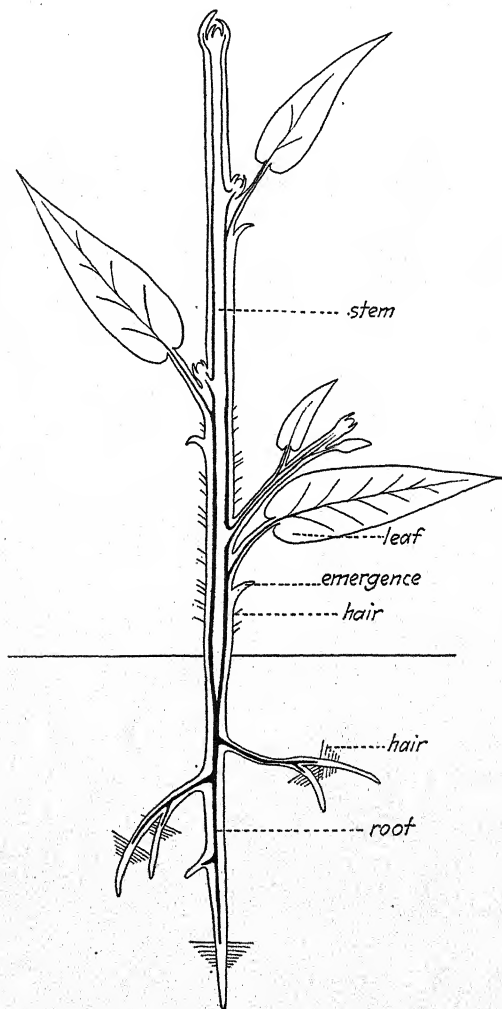


FIG. 1.—Diagram of plant body, showing fundamental parts.

mineral nutrients), the *phloem*. Xylem and phloem nearly always occur together, usually side by side radially, the phloem outermost (Fig. 2). These tissues together may form a solid rod, a hollow cylinder, a sheath of more or less symmetrically placed strands (Fig. 56), or a group of scattered cords (each consisting of xylem and phloem). Where the

arrangement of the vascular tissues is such that they enclose tissue of a different type, usually soft and loose, a central portion, the *pith*, is set off. Outside the external conducting cells and forming the outermost part of the stele are a few layers of non-conducting cells, the *pericycle*. The pericycle is usually limited externally by a definite uniseriate sheet of cells of peculiar structure, the *endodermis*. The vascular core is thus ensheathed by the pericycle in a way similar to that in which the stele is enveloped by the cortex.

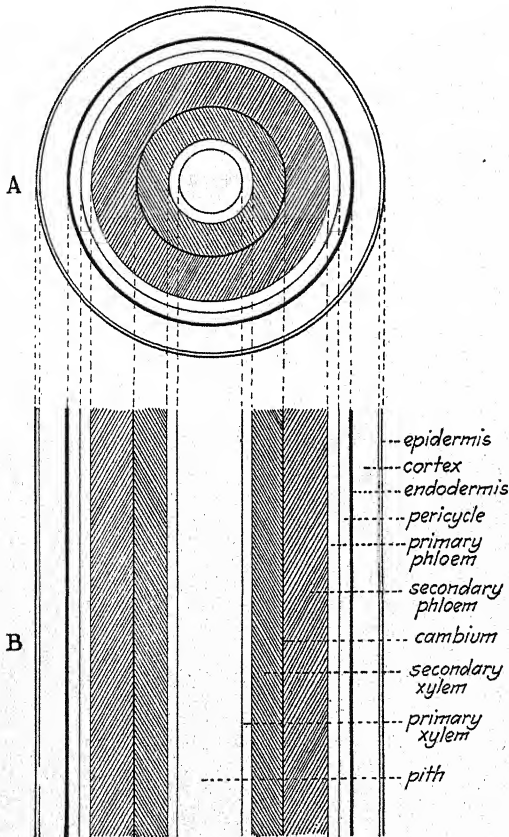


FIG. 2.—Diagram showing structure of axis. A, transverse section. B, longitudinal section.

Primary and Secondary Growth.—An axis complete in all the structural features above mentioned and with complete appendages is built up by growth at the growing points, situated at the tips of the axis. This first-formed body is known as the *primary body*, since it is built up by first, or *primary*, growth. Its tissues are, for the same reason, known as *primary tissues*; for example, the first-formed xylem is called *primary xylem*. In many vascular plants the primary body is reinforced

by a different sort of growth, which because it begins later and adds to the original primary tissues is called *secondary growth*. The tissues thus formed are termed *secondary tissues*. Secondary growth does not usually form new types of cells, but merely increases the bulk of the plant, especially of the vascular tissues, providing new conducting cells and additional support and protection. It does not fundamentally change the structure of the primary body. Primary growth increases the length of the axis, laying down its branching system and adding its appendages; that is, it builds up the new, or young, parts of the plant body. After the parts thus formed have attained full size, additional increase in diameter is secured only by secondary growth.

The secondary vascular tissues are formed by a specialized growing layer, the *cambium*, which arises between the primary xylem and the

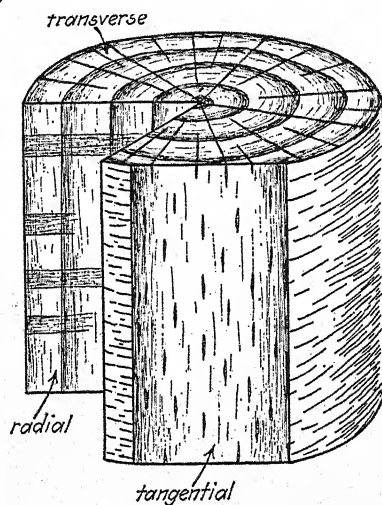


FIG. 3.—Diagrammatic sketch of a cylinder of wood, to show transverse, radial, and tangential planes of section.

primary phloem, and lays down new xylem and phloem adjacent to these. The secondary masses of xylem and phloem lie, therefore, entirely within the central cylinder and between the primary phloem and primary xylem. The newly formed xylem cloaks and ultimately completely surrounds the primary xylem and the pith, not changing the primary structure within, but burying it intact. The primary phloem and all other tissues outside the cambium are forced outward by secondary growth and may be ultimately more or less distorted or destroyed. The primary growth of a given region is completed in a relatively brief period, whereas secondary growth continues for a longer time, and in perennial axes may persist indefinitely.

Constitution of the Plant Body.—The root, stem, and leaves of a plant constitute its *organs*. These perform distinct, general functions for

which they are adapted by the kinds, proportion, and arrangement of the *tissues* of which they are composed. The tissues have more restricted functions, which are determined by the kinds of *cells* which constitute them. The plant body thus consists of cells, which are aggregated to form tissues, and these, in turn, are grouped together to form organs.

Methods of Studying the Anatomy of the Plant.—The minute structure of the plant body is learned chiefly from thin sections and from macerations in which the individual cells are freed from one another. For the adequate comprehension of the complex structure of most parts of the plant it is necessary that study be made of sections cut in more than one plane. For the axis—a cylindrical structure—three planes, each at right angles to the other two, are most useful; of these one is transverse to the long axis, the others parallel with the long axis, that is, longitudinal. Of the two longitudinal planes, that dividing the cylinder radially is the radial plane, and that at right angles to the radial plane is the tangential plane (Fig. 3). Sections cut in these planes are known as *transverse* (or *cross*), *radial*, and *tangential sections* respectively.

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CHAPTER II

THE CELL

Plants and animals are made up of living substance, *protoplasm*, and its secretions, the body of an organism being fundamentally a protoplasmic structure. This body is of complex organization in that, except in the simpler forms, it consists of many more or less independent parts or units. These parts, which are clearly units both of structure and of function, are termed *cells*. The structural distinctness of the cell—in plants especially—is due in large part to the presence of an outer layer, or coat, *the cell wall*, in plants usually firm, and often hard and thick; in animals, delicate or in some tissues perhaps lacking. The functional distinctness of the cell depends in part upon the presence and properties of an outer, limiting layer of specialized protoplasm lying just within the wall, the *plasma membrane*. The cell wall closely invests the protoplasmic unit, thus separating the protoplasm of one cell from that of adjacent cells. This separation is incomplete, however, since very minute perforations occur in the wall. Through these perforations extend processes of protoplasm, the *plasmodesma*, which secure the continuity of the living matter of one cell and that of contiguous cells. The protoplasmic body of an organism is thus a continuous living system, though its individual parts, the cells, are definitely set apart by cell walls.

Uses of the Term "Cell."—The term "cell" has, in its different uses, sometimes included and sometimes excluded the cell wall. As understood by the early students of plant anatomy, cells were the "boxes" formed by cell walls; these were seen only when the walls were thick and visible at low magnification, and contents were unknown. Later it was found that such a cell may have a living, protoplasmic content, the *protoplast*. When the protoplast was recognized as the essential part of the cell, the part concerned with the vital activities of the organism, attention was turned to this structure as "the cell." Because of this recognition of the protoplast as the fundamental unit, the term "cell" has since been used by many students to designate the protoplast alone. Perhaps in the more common sense, however, the term implies protoplast plus wall, these together constituting the obvious unit of structure, a unit for which there exists no term if "cell" is restricted in use to the protoplast alone. The term is further applied even to units of wall alone, as, for example, to the tracheid. The application of the term in this way is, of course, the same as to the protoplast plus wall, since in

such cases the protoplast has disappeared, leaving within the walls a cavity, the *lumen*. The use of the term "cell" to indicate both protoplast and wall is desirable in view of the intimate relation of the protoplast and wall—a relation the closeness of which is not yet understood, it being possible that the wall of a living cell is not merely a non-living, external secretion of the protoplast, but is itself partly protoplasmic in nature—and in view of the difficulties of expression otherwise involved. Such an understanding of the term is, of course, less strict than that underlying the frequently used definition of the cell as "an organized and more or less independent mass of protoplasm constituting the structural unit of an organism." Nevertheless, from the standpoint of anatomy, the term is better used in the looser and more comprehensive sense; it is so used in this text.

Cellular Complexity of Plants.—The primitive organism was doubtless unicellular, or, in a sense, non-cellular, and probably without an enclosing membrane or wall. The larger body of more advanced types is multicellular and the cells are limited by walls. The walls perhaps separate regions of activity of individual nuclei but certainly serve also for protection and support to the individual protoplasts and to the entire organism. Apparently, this walled condition is of great importance in large plant bodies both from the standpoint of mechanical stability and that of physiological delimitation. Clearly, adaptation to a terrestrial and aerial habitat and the maintenance of a large body under conditions unfavorable to protoplasm, have resulted in the specialization of the cell along various lines, especially those involving elaboration of the wall. Hence, there are to be found among higher plants many kinds of cells with much variety of function, structure, and arrangement, and with a great deal of complexity of wall structure. Variety, both structural and functional, of kind of cell; variety of relation of cells to one another; variety of arrangement of cells and of systems of cells with relation to one another and to the body as a whole—these give great cellular complexity to the more highly organized plants. It may be said, indeed, that in a general way the higher the plant, phylogenetically, the more complex its cellular structure.

Cell Arrangement.—Regularity of arrangement of cells is characteristic of tissues formed by growth from a cambium or from a similar meristem, that is, of so-called secondary tissues (Figs. 79, A; 80, A; 92, B). On the other hand, the cells constituting primary tissues tend to be without definite symmetrical arrangement (Figs. 43, 115). There are certain marked exceptions, however, to these statements. Regardless of regularity or irregularity of arrangement and of the method of origin, a group of cells may be compactly arranged, forming a close tissue continuous in one or more planes, or they may be more or less free from one another, with the resulting formation of *intercellular spaces* between

them (Figs. 30; 124; 132, *B, D*). Such spaces vary in shape with the shape and arrangement of the surrounding cells; in continuity; in abundance; and in size from microscopically minute openings to very large spaces which render the tissue in which they lie loose, spongy, and light (Figs. 139, *C, D*; 140, *A*). Such large intercellular spaces are often known as *air chambers*, *canals*, *lacunae*, etc. These terms are applied rather loosely, the larger spaces being called chambers and the much elongated ones canals. Spaces formed by the separation of walls followed by the retraction of the separated parts, or by spatial movements of the cells, are said to be *schizogenous*; for example, the resin canal of *Pinus* (Fig. 40, *B*), and the spaces of the aërenchyma of *Decodon* (Fig. 140, *C*); others, developed by the destruction of cells formerly occupying the position of the cavity are called *lysigenous*; for example, the oil cavities of citrus fruits (Fig. 40, *F*). In some cases cavities are formed by a combination of these two methods, and have been called *schizolysigenous* (Fig. 48, *C, D*). Some protoxylem lacunae are of the latter type. The intercellular spaces of a region may be without uniformity in size and shape, or in arrangement of the cells surrounding them; they may, on the other hand, form definite structural features of a tissue or organ because of the development about them of specialized limiting or supporting "walls," or layers of cells, such as the diaphragms of many aquatic plants. In most cases intercellular spaces appear to form definite systems and to constitute, perhaps, functionally conducting or aërating systems. Special types of intercellular space systems form ducts and canals (Chap. IV) with cells regularly arranged about them forming a sort of epithelial lining.

Cell Shape.—Because protoplasm is of semifluid nature, cells when free and independent tend to be spherical. But where young cells of essentially the same age lie together and grow in size, mutual contact and compression render them polyhedral with diameters and sides nearly alike. Further growth toward individual or group specialization for definite function leads to great variety in form—ovoid, ellipsoid, cylindrical, tabular, prismatic, lamelliform, fiber-like, and stellate or otherwise lobed or branched. There are, however, two chief types, the *subglobose*, or *polyhedral*, with diameters equal or only slightly different; and the *elongate*, with one diameter many times that of the others. Transitional types are, of course, numerous.

Cell Size.—In size also cells vary greatly; and size, like shape, is in part related to function. Extremely small cells do not occur among the higher plants. Parenchyma cells serving the usual functions, with normal protoplasm, have a transverse diameter of 0.01 to 0.1 mm. In pith, fleshy fruits, etc., the diameter of parenchyma cells may reach 1 mm. or more, and the cells then become readily visible to the naked eye. Fibers of wood and phloem range in length chiefly from 1 to 3 mm. in

the angiosperms, and from 2 to 8 mm. in the gymnosperms; cortical and pericyclic fibers are often much longer, and are, partly because of their considerable length, of particular economic importance, as, for example, those of flax and hemp. Fibers of excessive length—20 to 200 mm., and even much longer—occur in the Urticaceae and in certain monocotyledons. The largest cells known are latex cells of the type which form branching systems throughout a plant body (Chap. IV). Such cells, however, may not be individuals morphologically, since they are coenocytic and continue to grow almost indefinitely. Latex vessels are series of ontogenetically united cells.

Cell Development.—All cells are formed from preëxisting cells—or from nucleated protoplasmic masses—by division. Cell division is a complex process during which the nucleus and cytoplasm are each divided into two parts, usually equal and alike. In this division the wall is not directly involved. In the newly formed cells the plasma membranes are not readily distinguishable, and hence a visible plane of separation is at the very first lacking or scarcely detectable. Very early, however, the new wall appears along this plane as a delicate membrane. Thus, cells while still very young, are provided with walls. Such young cells are nearly always smaller than mature cells, and are of more uniform size and shape, usually isodiametric, and very simple in structure. Elaborate shape, complex structure, and very large size are not to be found

among young cells. Growth of cells, therefore, involves increase in size and the development of special shape and structure. Since the wall is present from a very early stage, both protoplast and wall are involved in these changes. The protoplast, as the active part of the cell, initiates the changes, the wall becoming adapted to the changing protoplast. While changes in size and shape are taking place, the physical and chemical nature of the wall is such that these accommodations are readily made; only after cell maturity is attained is a fully developed and unchanging wall present. In the maturing of the protoplast many changes occur. These are, briefly, the reduction of the proportionate size of the nucleus; the development of less dense or less richly granular cytoplasm; the appearance of vacuoles which increase in

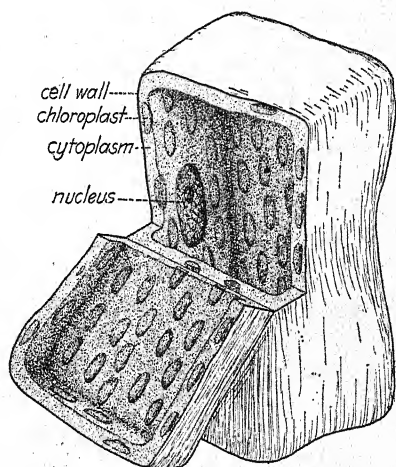


FIG. 4.—Diagrammatic representation of mature mesophyll cell opened to show central vacuole (filled with cell sap), nucleus and plastids embedded in the peripheral cytoplasm; wall thin. (Based on Zea.)

size, and, in most cases, ultimately fuse to form one large central vacuole which restricts the cytoplasm to a peripheral position adjacent to the wall; the increase of plastids in size and number, and the development of special types of these structures (Figs. 5; 6, A-C; 25, A-C).

Gliding Growth.—With the growth of the protoplast in size, the wall is increased in extent and thickness (p. 23). In the attainment of certain cell shapes and sizes (fiber and branching types especially) the walls of the growing cells, or certain portions of the walls, slide over one another. This sliding or *gliding growth* begins with the splitting of the primary wall into the portions belonging to each of the contiguous cells and is followed by a slipping along the plane of separation. Such movement results in the displacement of certain parts of a cell, or perhaps in some cases of the entire cell, in relation to the abutting cells. New areas of contact are established, and in many cases these areas are between cells not originally contiguous. Movement of this type should not be confused with spatial displacement resulting from enlargement of tissues in meristematic growth. Gliding growth may accompany such changes in position, as in the dislocation and distortion of tracheids by vessel enlargement in the ontogeny of secondary wood.

Gliding growth is a characteristic feature of developing tissues of vascular plants. It occurs in the maturing of tracheids and fibers from cambium cells, where the elongation of the tapering ends (Fig. 74), or perhaps of the entire cell, pushes the ends farther between the adjacent cells (Figs. 73, 76). Elongation of maturing fibrous cells of various types by gliding growth brings about greater overlapping than was present in the very young cells, and interlocks them strongly, adding greatly to the mechanical value of such cells as strengthening elements.

THE PROTOPLAST

✓ The cell may be considered to be separable both structurally and functionally into the central protoplasmic unit, the *protoplast*, and the surrounding membrane, the *cell wall*. The protoplast is the cellular unit of the body of protoplasm which fundamentally constitutes the organism. This living substance, protoplasm, as now understood, is not a definite compound, but consists of a number of compounds in complex organization. These compounds are colloidal in nature and vary both in kind and in proportion in different plants and in different tissues in the same plant. The protoplast may be further described as an organized protoplasmic unit which contains specialized portions of various kinds, and also non-living *inclusions*, organic or inorganic, such as starch grains, oil globules, protein granules, and crystals of many kinds. These non-protoplasmic inclusions are sometimes considered not to be a part of the protoplast. However, aside from the possibly intimate relation of these substances to the physiological activities of the

protoplast, they constitute, if only as inclusions, a part of the protoplast as a structural unit. The cell wall is usually considered as definitely distinct from the protoplast; that such may not be the case, however, is possible. In the discussion of the nature of the wall (p. 19), this aspect of cell structure is further treated.

Organization of the Protoplast.—The protoplast possesses in nearly all cases a very highly organized part, the *nucleus* (Figs. 4, 5). This is proportionately small, more or less rounded in shape, and apparently functionally of the greatest importance in the activities of the cell. To the remaining portion of protoplasmic material the term *cytoplasm* is

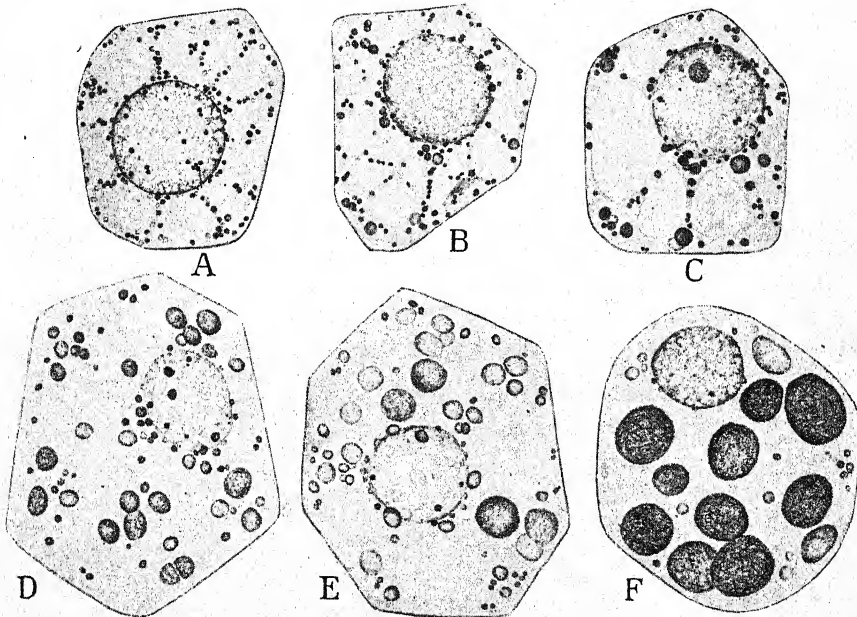


FIG. 5.—The development of a mesophyll cell in *Zea*. A–F, successive stages: the nucleus decreases in proportionate size; vacuoles appear, enlarge, and fuse; chloroplasts develop from proplastids. (After Randolph.)

given. This itself has portions of different degrees of specialization which are given over to segregated functions.

The Plasma Membrane.—A thin, outermost layer of the cytoplasm differs from the remainder in its hyaline and non-granular nature, and also is apparently very different in function. This is the *plasma membrane*, or *ectoplast* (Fig. 11). In the living, unplasmolized cell this layer is not readily visible, owing to its delicacy and lack of distinctness as a layer, and to its close association with the wall. (It is not shown in Figs. 4 and 5.)

The Plastids.—The more conspicuous portions of the cytoplasm are the *plastids*. These are differentiated bits of protoplasm—"organs,"

or areas of metabolic activity associated with particular functions. In size they are small, and generally many occur in a cell (Figs. 4, 5, 7). In shape they are variable, but the roughly rounded types are most common. Spherical, ovoid, discoid, granular, rod-like plastids all occur frequently; very large plastids of peculiar shape are present in many of the algae.

Occurrence.—Plastids may be found in all living cells of a plant, and probably are present in every cell in the early stages of development. Later they become restricted to certain cells, and are abundant only in those which have specialized functions, such as photosynthesis, storage, and color manifestation. Plastids do not occur in the fungi, bacteria, or myxomycetes, and only rarely in animals.

Origin and Structure.—Plastids multiply freely by division, and in this way the large numbers present in some cells are in part secured. Plastids are present in very young meristematic cells (Fig. 5, A), where they are very minute, the smallest being at the limit of microscopic visibility.

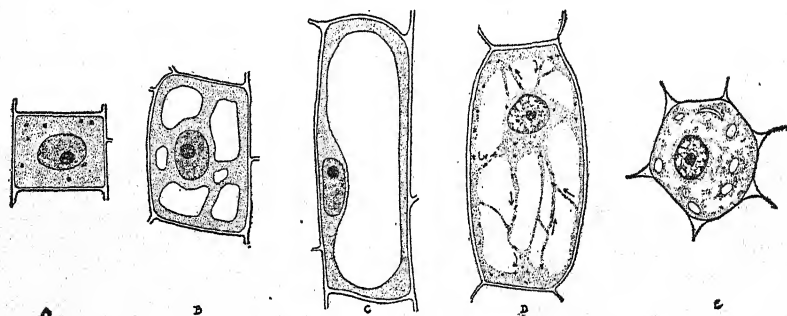


FIG. 6.—A-C, diagram of a plant cell in three successive stages of development: the vacuoles increase in volume and fuse and the cytoplasm becomes limited to the parietal region. D, cell of stamen hair of *Tradescantia*, indicating direction of streaming movements in the cytoplasmic strands. E, parenchyma cell from cortex of *Polygonella*, showing nucleus, plastids, and scanty cytoplasm. (After Sharp.)

At this stage they have been called *proplastids*. Commonly plastids multiply by division when mature or nearly so. Possibly, multiplication by division takes place also at the proplastid stage, or at a stage still earlier. New plastids arise freely from preëxisting plastids. Whether or not plastids also arise *de novo* from protoplasm is uncertain because of the extreme difficulty of observing proplastids. In structure, the plastid consists of a foundation of protoplasm, very loose and mesh-like in some forms, dense and compact in others. In this there are contained various complex substances, often highly colored, in the form of crystals, granules, globules, or in solution or suspension in the protoplasm itself.

Types of Plastids.—Several fairly distinct types of plastids occur, but all are of similar nature. They fall into two chief classes, distinct in function and color: *chromoplasts*, colored plastids; and *leucoplasts*,

colorless plastids. The term *chromatophore* is sometimes used as synonymous with chromoplast; but since this term has several somewhat different meanings—a non-green chromoplast, a highly specialized chloroplast, etc.—the term *chromoplast* is preferable.

Chromoplasts.—Physiologically, the most important type of chromoplast is the *chloroplast*. These plastids are green and mostly spherical or discoid (Figs. 4; 5, *F*), and constitute the well-known photosynthetic “organs.” In some cases, as in the brown and red algae, the green color

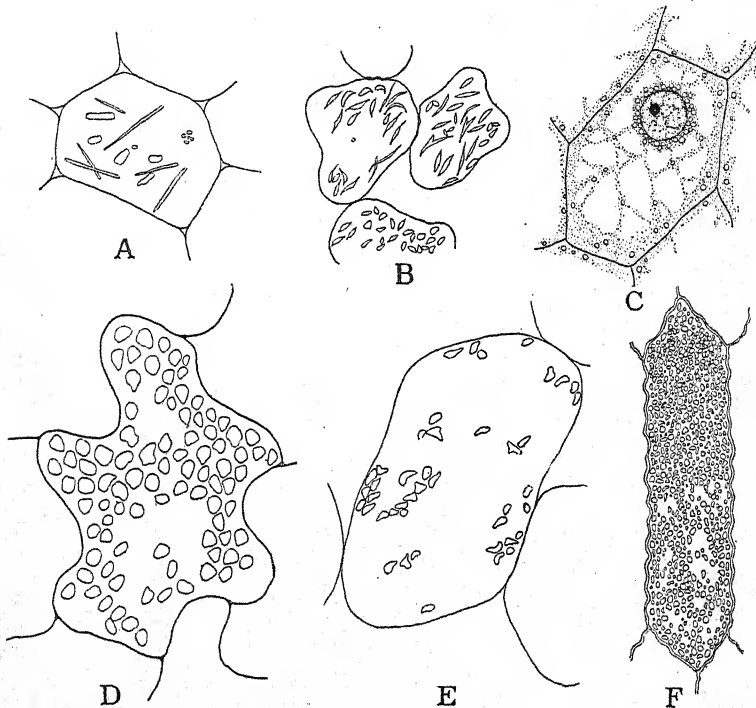


FIG. 7.—Plastids. Chromoplasts: A, in cortex cell of root of *Daucus*; B, in pulp cells of fruit of *Arisaema*; D, in cell of petal of *Forsythia*; E, in pulp cells of fruit of *Lycopersicum*; F, in cell of corolla of *Taraxacum*. Leucoplasts: C, in endosperm cells of *Zea*.

of the chloroplast is masked by the presence of other pigments. The other chromoplasts range in color from yellow to red, and in shape are very variable, being chiefly irregular. Granular and angular types are common, and even forked types occur (Fig. 7, A, B, D, E, F). The irregular and sharp-pointed characters are largely due to the presence of crystals of coloring matter within the plastids, as in *Daucus* (Fig. 7, A). The function of these chromoplasts is obscure. They are, of course, color bearers in flowers and fruits, but they occur also in other regions

where color in itself serves no apparent function, as in the root of the carrot. In flowers and fruits they have not been shown to be of value in metabolism.

Leucoplasts.—The term *leucoplasts* is commonly applied to all colorless plastids. The minute plastids of this type which occur in meristematic cells represent the early stages of other types of plastids. These are better known as proplastids, the term leucoplasts being reserved for mature colorless plastids. Leucoplasts vary in shape, being frequently elongate and rod-like. They are concerned with food storage and possibly with other functions. The type of leucoplast associated with starch-grain formation in storage regions is known as *amyloplast* (Fig. 7, C). The leucoplasts of hairs and of other epidermal cells are probably, in part at least, degenerate or dormant plastids of other types.

That all plastids are alike in nature is clear from the readiness with which they are transformed one into another. For example, the chloroplasts of young fruits and of developing petals may become the chromoplasts of the ripe fruit and of the mature flower respectively; the leucoplasts of a potato tuber become chloroplasts on exposure to light.

Occurrence of Plastid Types.—Chloroplasts may occur in any part of a plant which is exposed to the light; they also occur in some tissues which are apparently without light, such as the wood of many Rosaceae and Ericaceae, and in embryos and endosperm, as in the seeds of some citrus fruits. Red and yellow chromoplasts likewise may occur in any organ of the plant, and their presence is not related to the presence of light. They are chiefly to be found, of course, in flowers and fruits. Leucoplasts occur chiefly in parts not exposed to light.

Further statements concerning the distribution and the function of plastids are to be found in the discussion of various tissues, tissue systems, and organs, such as collenchyma, the cortex, and the petal.

Other Cytoplasmic Structures.—Many protoplasmic bodies smaller than plastids occur in cytoplasm; these are known as *chondriosomes*, *mitochondria*, etc. Some of those known as chondriosomes are proplastids. The nature and the distribution of these smaller cytoplasmic structures, however, lie outside the field of the present treatment.

Vacuoles.—The cytoplasm of mature cells contains one or more large cavities known as *vacuoles*. Conspicuous cavities are not present in very young cells, but develop as the cell matures, appearing as one or several very small cavities and enlarging and fusing until in the mature cell there is usually one large central vacuole which restricts the cytoplasm to a thin layer lining the wall (Figs. 4; 6, C). The nucleus, plastids, and most inclusions are contained in this peripheral layer. Frequently strands of the cytoplasm extend from the outer layer as irregularly anastomosing branches through the central vacuole; in such cases the nucleus may occupy a median position in the cell.

Cell Sap.—Vacuoles are filled with *cell sap*, usually a clear, watery liquid. This liquid is non-protoplasmic, and consists of water with various substances in solution—inorganic salts, carbohydrates, proteins, amides, alkaloids, pigments, etc. These substances may be mineral nutrients, elaborated food, waste products, or substances of unknown relation to metabolism. The significance in the physiology of the cell of these substances dissolved in the cell sap is not well understood, but it is highly probable that they are intimately concerned with the cell organization. The group of pigments known as anthocyanin is frequently present in the cell sap, and is responsible for the coloring of plant parts which ranges through violet, blue, and blue-red, the color varying with the acidity or the alkalinity of the cell sap. Dissolved xanthin renders the cell sap yellow in a few cases, but yellow coloring is usually given by chromoplasts.

Autumn coloring is not due primarily to the presence of chromoplasts or of anthocyanin. The yellows are due to broken-down chlorophyll and disorganizing plastids and cytoplasm, the reds to the presence of a pigment said to be formed in the presence of light from sugars and the products of chlorophyll disintegration. Other colors are the result of various combinations of yellows and reds with the green of chlorophyll, the brownish color of the changing cell walls, and with other colored substances.

✓ **Inclusions of the Protoplast.**—Many kinds of solid particles, organic and inorganic, as well as such substances as oils, gums, resins, etc., are frequently present within the protoplast, either in the cytoplasm or in the vacuole. These represent, like the dissolved substances, food products, such as starch and aleurone grains; waste products, such as crystals; and other substances of doubtful or unknown function, such as tannin, latex, alkaloids, etc. Gums, resins, tannin, etc. are often present in the lumina of non-living cells; for example, in the heartwood of *Sequoia* (Fig. 80) and *Swietenia*, and in cork cells of other trees. Some of these substances, as, for example, starch, occur in most plants; others are characteristic of certain large or small groups of plants, and are lacking in others.

Crystals.—Crystals of various chemical nature occur freely in plant cells; of these, salts of calcium, chiefly calcium oxalate, constitute the majority. Crystals of other salts of calcium and of various other inorganic substances, such as silica and gypsum, occur less frequently; and crystals of many organic substances, such as carotin, berberin, and saponin, are frequent. All parts of the plant may contain crystals, though these structures are more abundant in certain regions, as in the pith, cortex, and phloem, than in others. There are many forms of crystals (Fig. 8). Of these, solitary, rhombohedral crystals, sheaf-like bundles of long acicular crystals known as *raphides* (Fig. 8, E), and

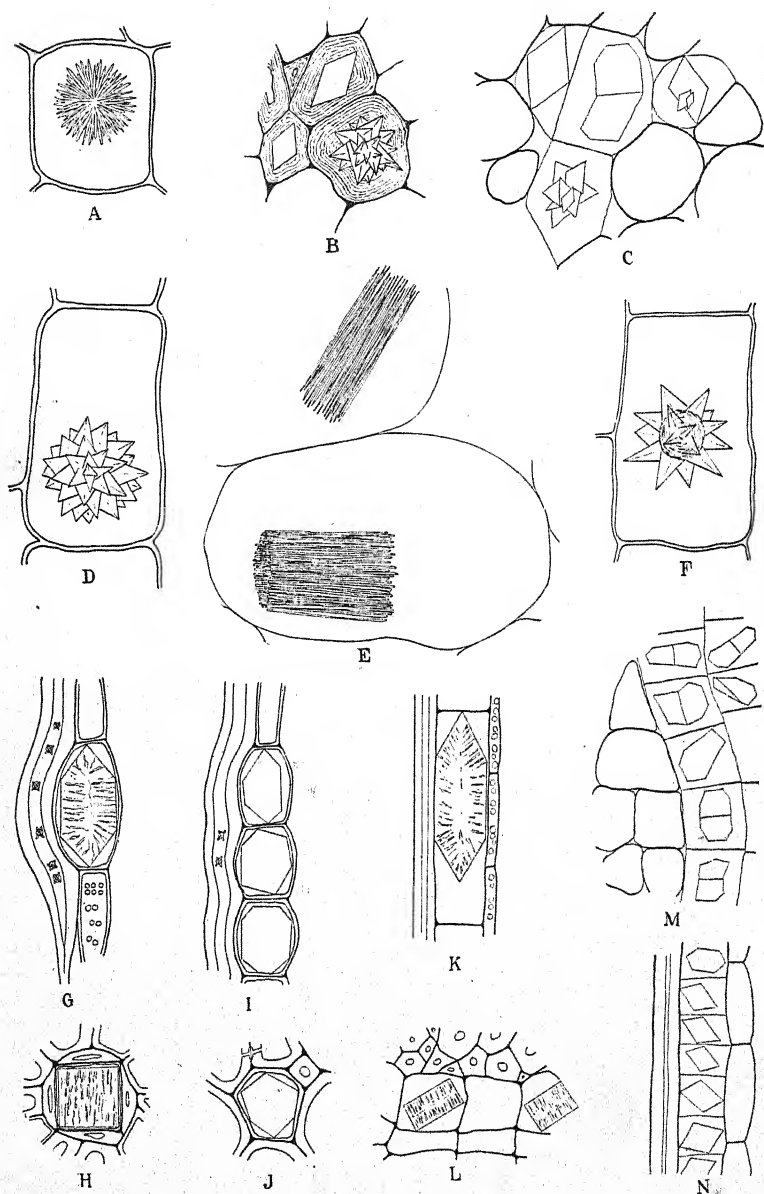


FIG. 8.—Crystals. A, druse in cortical cell of stem of *Viburnum Lentago*. B, druse and rhombohedral crystals in stone cells of nutshell of *Carya glabra*. C, solitary and grouped crystals in pith cells of *Populus grandidentata*. D, druse in cortical cells of *Carica Papaya*. E, "bundles" of raphides in pulp cells of fruit of *Smilacina racemosa*. F, druse with organic center, in phloem parenchyma cell of *Juglans nigra*; G, H, longitudinal and transverse sections of crystal in wood parenchyma of *Carya Pecan*; I, J, longitudinal and transverse sections of crystals in wood parenchyma of *Juglans nigra*; K, L, longitudinal and transverse sections of crystals in phloem parenchyma of *Tilia americana*; M, various forms of crystals in phloem parenchyma of *Pyrus Malus*; N, rhombohedral crystals in phloem parenchyma of *Salix nigra*.

clustered crystals in globose masses called *druses* (Fig. 8, *A, B, D, F*) are most common. Solitary needle-like crystals, small prismatic crystals, and minute crystals called crystal sand are other frequent types.

One form of crystal may occur in a given cell—the usual condition where crystals are clustered—or two or more types may be found in the same protoplast. Many inorganic crystals involve organic matter in the course of their formation. The larger crystals of xylem often show this condition (Fig. 8, *G, H, K, L*), and druses frequently contain a prominent organic center (Fig. 8, *F*).

The large crystals of somewhat various shapes—prismatic, rhomboid, etc.—occur chiefly in fibers of xylem and of phloem and in parenchyma cells associated with fibers. Raphides occur in thin-walled, mucilage-containing parenchyma cells of soft tissues, such as storage parenchyma of underground parts, fruit pulp, and the tissues of aquatic plants generally. They are present in monocotyledons chiefly. Druses are characteristic of parenchyma cells of cortex and pith, especially of stems and petioles; they also are abundant in phloem.

Crystals lie chiefly in the protoplast, or in the lumen when the protoplast has disappeared, as in fibers. Occasionally, they are found embedded in the cell wall; more frequently they are suspended in the lumen by projections of the walls. These projections are beam-like; or are sac-like, completely covering the crystal and holding it in a central position. Large crystals may fill the lumen and in such cases determine the interior contour of the wall (Fig. 8, *B*); in elongate cells the lumen may be filled at a given level only (Fig. 8, *G, H*).

Cells may be given over entirely to crystal storage, and the protoplasts become much reduced or disappear, but typical active cells may also contain abundant crystals. The early stages of crystals are found in very young cells; thus, apical meristem often contains young druses.

In large part, inorganic crystals are probably waste products, the result of metabolic processes. Their development in tissues which soon cease to be functional, such as pith, cortex, and secondary phloem, is suggestive of this. It is possible that raphides, where they occur in tissues filled with food and in aquatic plants which are otherwise mechanically unprotected, may be to some extent of protective value against snails and other small animals.

Starch.—Food materials are present either as transitory material or in the more or less permanent form of storage particles. Newly formed food may be in solution or exist as solid particles. Starch grains are the most common kind of solid food material found. They are of numerous types and vary in size and in form over a considerable range (Fig. 9, *B, C, D, E, G, H*). In shape they are mostly rounded or oval. Crowding, results in the formation of angular shapes (Fig. 30, *B*), and symmetrical, polyhedral grains are characteristic of some plants. Other plants

possess compound grains which much resemble simple grains, but show their compound nature when broken up into parts which are minute simple grains. All grains in a cell may be simple or compound, or both types may occur in the same cell (Fig. 9, D). Structurally, starch grains consist of a series of roughly concentric layers around a more or less central portion of somewhat different nature, the *hilum*. The layering varies greatly in distinctness, being usually obscure. The hilum is

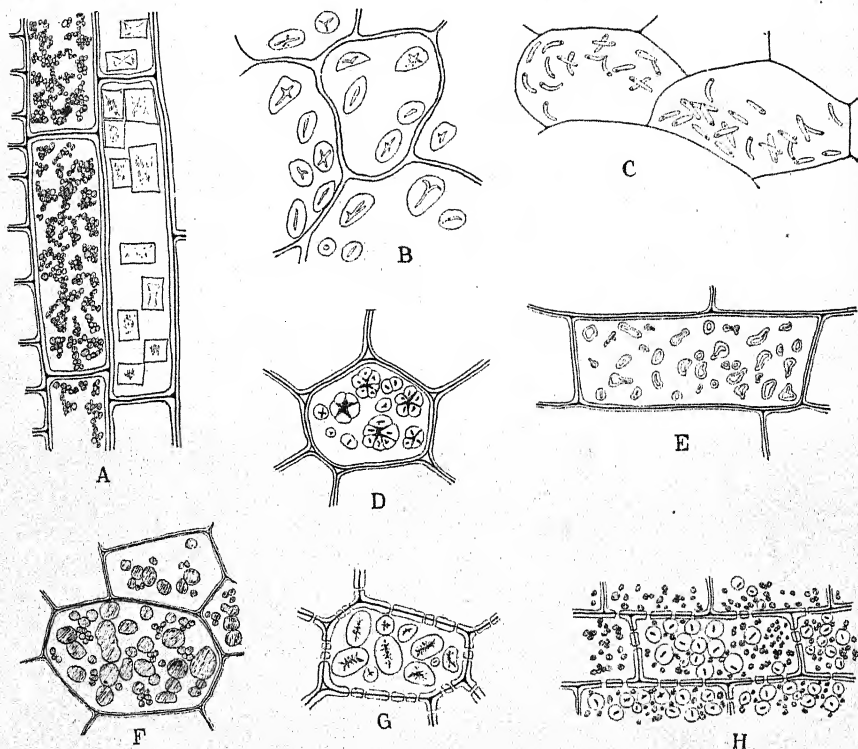


FIG. 9.—Starch grains and tannin. Tannin: A, in phloem parenchyma of *Pinus* (also crystals); F, in pith cells of *Fragaria*; H, in ray cells of wood of *Pyrus Malus* (also starch grains). Starch grains: B, in pith cells of *Alsophila*; C, in outer pericarp of *Musa*; D, in cotyledon of *Pisum*; E, in ray cell of phloem of *Ailanthus*; G, in cotyledon of *Phaseolus*.

rounded or angular, sometimes lobed, forked, or stellate, and is highly refractive to light. By the presence of hila and by staining properties starch grains may be distinguished from plastids and other protoplasmic bodies, and from other solid particles.

Starch grains are first formed within chloroplasts and may often be found in that position; leucoplasts in storage cells build up starch grains within themselves from translocated food brought from green cells. Starch grains are thus formed both primarily and secondarily within plastids. It is not known with certainty whether, when a grain is mature,

it is freed from the plastid, or is still surrounded by a very delicate layer of plastid substance.

Nitrogenous Inclusions.—Solid nitrogenous particles such as *crystalloids*, or *protein crystals*, are frequent in seeds and in other storage organs, such as bulbs and tubers, as in the potato tuber; and *aleurone grains* are often found in seeds where definite layers of cells are filled with them, as in the corn fruit (Fig. 10). Crystalloids and aleurone grains are rare elsewhere. Tanniferous bodies are abundant in many plants, especially in the cortex and phloem (Fig. 9, A, F, H). They occur chiefly in parenchyma cells but may be found in other cells, such as those of collenchyma and cork. To their abundance in the phloem of oak, hemlock, and other trees is due the value of the bark of these trees for tanning. Tanniferous bodies are small, granular, or rounded particles, often more or less fused in masses. Tannin may be mixed with or dissolved in gummy or mucilaginous masses in the protoplast. Other solid or semi-solid substances, such as resins, gums, mucilages, fats, etc., occur frequently.

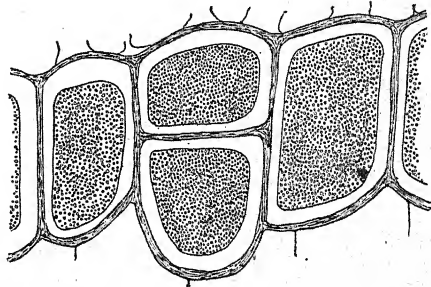


FIG. 10.—Aleurone grains in endosperm of *Zea*.

THE CELL WALL

In vascular plants only certain cells concerned with reproductive processes and early embryology are naked. All others are enclosed by cell walls immediately after their formation. This wall, although at first very thin and delicate, is modified in various ways as the cell matures. The more important of these changes are increase in extent and in thickness, and modification of grosser physical structure, such as the absorption of the end walls of porous vessels. The presence of the wall, especially after the earliest stages of development, renders cellular structure in plants very distinct—a feature in strong contrast with the condition in animals where the walls are more or less obscure and the limits of the protoplast, therefore, less readily discernible.

Origin and Nature.—The cell wall is commonly looked upon as a secretion of the protoplast, laid down upon its surface. Strictly as such, the membrane would be a non-living layer. Although this is the view now generally accepted, the opinion is held by some that the wall is, to some extent at least, composed of protoplasmic material, and hence is itself a portion of the living cell. Certain facts of structure and behavior of cells are at present more readily understood on this basis; others, however, seem difficult of interpretation if the wall be a living adjunct of the protoplast. Both conditions may of course exist.

Although when the protoplast was first recognized as the fundamental functional element, the wall was believed to be a layer of secreted material, the opinion that it is a structure primarily or partly living in nature soon replaced this early view. This later view developed from studies of nuclear division and of the formation of spindle fibers and the cell plate, and persisted until the details of formation of the latter structure, and of its behavior in late stages of cell formation, were much better known. The cell plate is cytoplasmic in nature and the wall appeared to be a direct transformation thereof, and therefore fundamentally living in nature. However, it is now generally believed that the cell plate splits, probably forming the plasma membranes of the daughter cells, and that the wall is laid down between them (Fig. 11). That this new wall is of double nature is not obvious in early stages, or even, in most

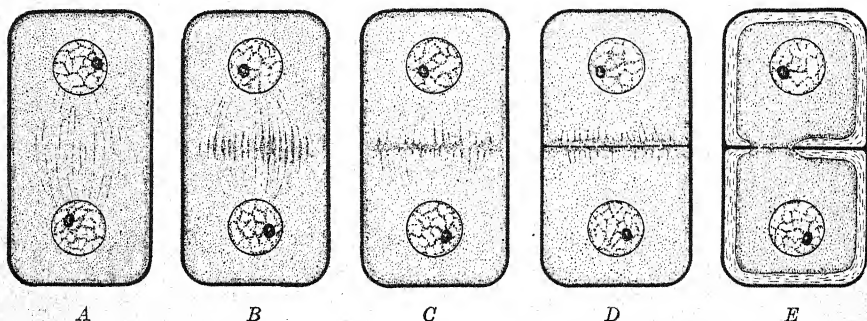


FIG. 11.—The development of the cell wall in a vascular plant, as described by Timberlake and Allen. *A*, telophase of mitosis in meristematic cell. *B*, appearance of swellings on the achromatic fibrils. *C*, fusion of the swellings to form an equatorial cell plate; fibrils disappearing. *D*, deposition of new primary wall (middle lamella) between the halves of the split cell plate; the two portions of the cell plate become the plasma membranes of the daughter cells. *E*, deposition of a secondary wall layer between the plasma membrane and the middle lamella, except in the region of a large pit; the closing membrane of the pit has fine perforations. Primary wall drawn in solid black; cytoplasm stippled; plasma membrane densely stippled; secondary wall shaded with lines.

cases, later; but when a group of cells begin to separate, "rounding up" from meristem, or otherwise developing intercellular spaces, the early formed wall becomes clearly two-layered and splits into two equal portions. There are a few cases where cell walls or portions of wall appear, though doubtfully, to be built up by transformation of cytoplasm either through replacement or by chemical change.

The theory that the wall is composed of living substance was based at first upon this idea of transformation, the living material being gradually replaced by non-living, some of the former being retained, however, so long as the protoplast persists. In a wall of such mixed nature, the portions of cytoplasm persisting have been considered to form a meshwork in which lie embedded the particles ("granules," "spherules," "droplets," "dermatosomes," "micellae") of carbohydrate or similar nature. Where

the protoplasmic content is small in amount, the meshwork is of cord-like strands; where it is large in amount, the meshes are merged into a semi-fluid mass suspending bits of non-living substance. A recent view maintains that the wall of a living cell is a colloidal network, the framework of which is of cellulose and hemicelluloses, the meshes containing projections of the protoplast which are intimately connected with the plasma membrane. Certain it is, whether the outer layers of the protoplast penetrate the contiguous cell wall or not, and whether the wall is in any degree a part of the living substance of a plant, that there is a most intimate relationship between the wall and both the cytoplasm and the nucleus during the formation of the wall. Particularly is this true during the increase in size and thickness and the modification of the wall substance.

Plasmodesma.—The relation between cell wall and protoplast is rendered very close by the penetration of the wall by delicate threads of cytoplasm which pass through the wall between two cells, thus bringing into direct contact the protoplasts of adjacent cells. These fibrils, known as *plasmodesma*, lie in minute passages which in most cells constitute the only breaks in the continuity of the wall (Figs. 12, 13). The presence of these connecting strands in plant cells generally and their distribution in the walls have been poorly understood and too little recognized, but it seems to have been clearly demonstrated that cytoplasmic intercommunication is characteristic of living cells, or at least of all such as retain cellulose, or un lignified walls. The fact that these connections are so rarely seen and their presence so often doubted is without question due in most cases to their extreme fineness and to the need of special technique for demonstration. Plasmodesma are most often seen in thick-walled cells, especially those of endosperm, where they are long and of comparatively large diameter (Fig. 12, B, E). Aside from these cases they are said to be generally largest in mosses, somewhat smaller in ferns, and still smaller in seed plants. In some angiosperm genera, however, they are large, as in *Viscum*; whereas in others, such as *Begonia*, all attempts to demonstrate them in vegetative tissue have been futile. The failure to find them in such cases is probably due to their excessive fineness. In ferns and gymnosperms they have been clearly demonstrated in living cells throughout the plant.

These connecting threads are now generally believed to be present from the beginning, probably arising in some manner soon after nuclear division. That they are persistent portions or derivatives of the spindle fibers is, however, very doubtful. That they are cytoplasmic projections secondarily perforating the delicate young wall seems not impossible. The number of plasmodesma in a young cell is very great. As the cell develops the number may be reduced by the obliteration of part of the strands. The distribution over the cell is not uniform. The strands

occur in large part in groups, the distribution of which is determined by the shape of the mature cell and by its points of contact with its neighbors. The larger groups occur in small areas, which, as wall thickening goes on, remain thin, each area becoming a pit. Other fibrils occur in smaller

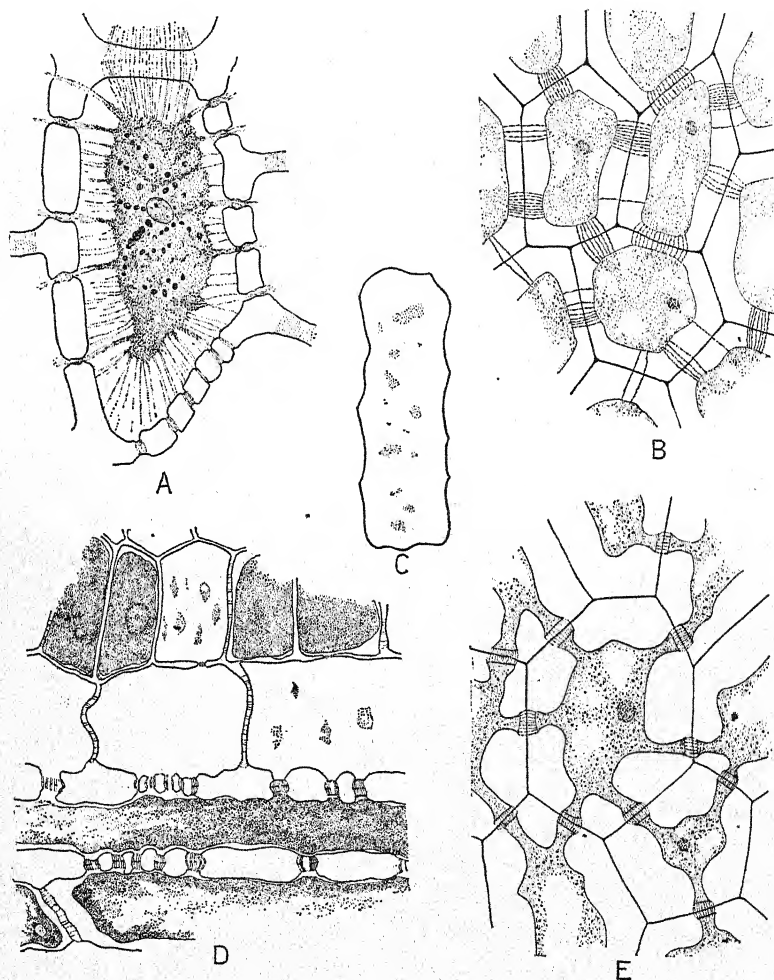


FIG. 12.—Plasmodesma. A, in a cell from the petiole of *Marattia* (the cytoplasm plasmolyzed). C, in a cortical cell of *Ophioglossum*, the strands seen "end en." D, in cells of root cap and adjacent cortex of *Vicia Faba*. B, in endosperm of *Diospyros* (persimmon). E, in endosperm of *Phoenix* (date). (A and C after Poirault; D after Gardiner and Hill.)

groups, or solitarily in the thicker portions of the wall. In the splitting of the cell walls in loose-tissue formation they have been seen to be divided and the halves to disappear, the channels being filled either by a secretion of the protoplast or by the swelling of the surrounding wall. In dead cells, the plasmodesma disappears with the protoplast, in rare cases

the channels being indistinctly seen afterward, as in tracheids. Plasmodesma are especially abundant in meristems, phloem, storage tissue, and in such living conducting cells as those of vascular rays (Fig. 13). They bear a close resemblance to the connecting strands of sieve tubes; in fact, the latter strongly suggest merely enlarged plasmodesma.

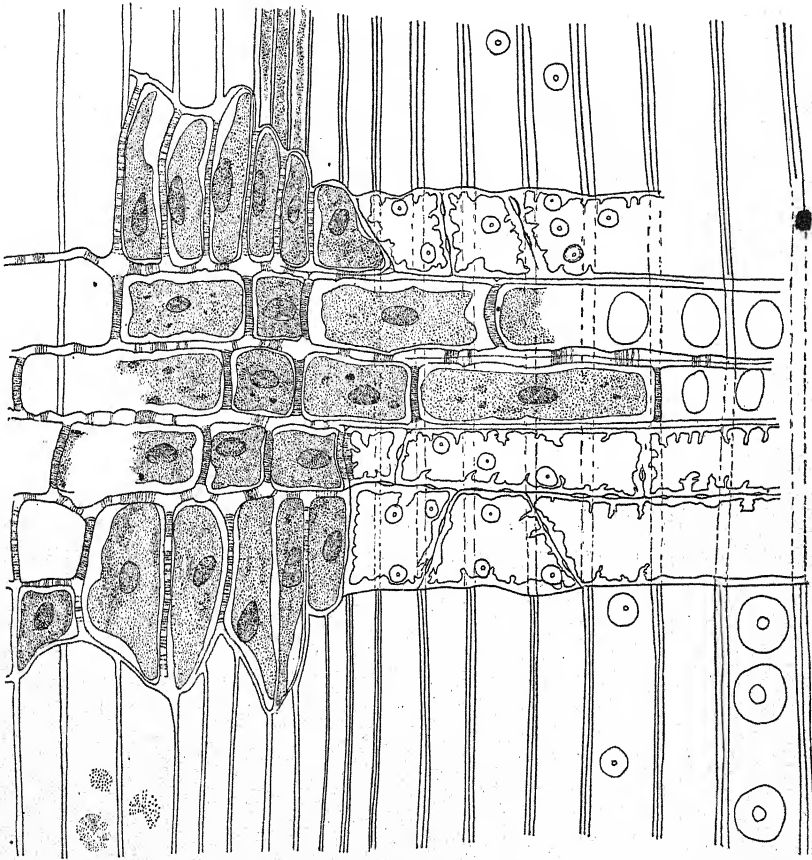


FIG. 13.—Plasmodesma in all living cells of the vascular ray in the cambium region, *Pinus sylvestris*. (After Gardiner and Hill.)

Development of the Cell Wall.—In growing cells which are destined to become large or highly specialized, the wall increases greatly in extent. This increase is possibly the result of a stretching accompanied by a simultaneous deposition of new material in the form of thin plates, a method of increase known as *apposition*; or it is brought about by the addition of new particles to those of the existing wall, the new particles forming among the previously existing ones, a process called *intussusception*. Either of these processes may be effective locally in the cell, or throughout its surface; both may be concerned in the thickening of the same wall.

Intussusception seems to be much the less common and to occur chiefly in the early stages of wall growth; apposition is believed to be the method by which thick walls are chiefly built up, except perhaps in free cells, such as spores and pollen grains.

Increase in thickness which is not the result of intussusception is either *centrifugal*—away from the center of the cell, that is, outside of the original wall; or *centripetal*, toward the center, inside of the preëxistent wall. The former method is of minor importance, since it occurs only among cells with free surfaces—spores, pollen grains, some hairs and other epidermal cells, and certain cells abutting on air chambers. Even in many of these cases it is doubtful if the thickening is actually centrifugal. The walls of spores may be in part thickened by additions by ~~the~~ tapetal fluid or mother-cell cytoplasm, but the nodules, granules, etc. on hairs can be explained only as products of the protoplast itself. Both these and the thickenings of pollen grains have been considered to be formed by intussusception. The nodules on hairs are mostly very minute and serve no understood function unless it be that by retaining a film of air they prevent wetting of the surface. Centripetal thickening builds up the walls of most thick-walled cells. The resulting walls are very diverse in character and in thickness. The apparently layered condition of most thick walls suggests that apposition is the method by which the process takes place, but it seems likely that intussusception is also concerned in the process.

Wall Structure.—Thick walls nearly always show in section a definite banding called *stratification* (Figs. 8, B; 20, J; 32, G). This is due to the presence of lamellate structure, the layers varying in optical qualities because of differences in water content, perhaps in arrangement of particles, in chemical nature, or in a combination of these ways. Besides this concentric structural layering there are sometimes seen in surface view of thickened walls markings known as *striations*, a system of delicate lines running obliquely or spirally in the wall. Whether such lines are due to the arrangement of particles within the wall or to the presence of strips of thickening material, laid down spirally, or to some other cause, is not known. Striations are usually seen only after special staining treatment. They should not be confused with tertiary thickenings (Fig. 14), elongate pit mouths (Fig. 19, A), or microscopic wall checking (Fig. 19, H).

Both stratification and striation are of less importance than a grosser division of the thick wall into *primary*, *secondary*, and *tertiary* layers, or *walls* (Fig. 14). Distinction between these layers is chiefly that of extent over the surface of the protoplast and of difference in chemical nature. The primary wall is the first-formed wall, continuous about the protoplast except for the plasmodesma perforations; the secondary wall is laid down upon the primary wall, that is, centripetal to it, and differs

from it markedly in that it is less continuous, the pits and, in some cells, larger areas, forming gaps in its extent. The tertiary wall lies upon the secondary, covering a relatively small proportion of the area, being made up of spiral bands loosely or tightly coiled. In many types of cells no sharp distinction can be made between a primary and a secondary layer. The primary wall, however, may be said to be the wall present until the protoplast has reached approximately its mature size and shape. It does not show pit perforations (though locally modified to form the closing membranes of pits), and differs from the secondary usually in being thinner and more dense, with little or no stratification. It is

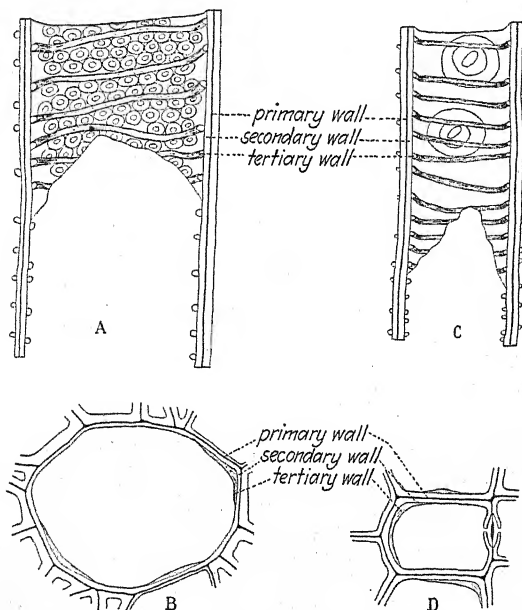


FIG. 14.—Primary, secondary, and tertiary walls. A, B, longitudinal and transverse sections of vessel of *Tilia americana*. C, D, longitudinal and transverse sections of tracheid of *Taxus brevifolia*.

further usually different in chemical nature, though the primary and secondary walls may be alike in this respect, in which case distinction between them is difficult. Cells with thin walls devoid of layering often show definite pitting. In such cases no distinction of primary and secondary walls can be made, though the presence of pits may suggest that both are present. If it is desirable to call such a wall wholly primary, the definition of primary wall may be modified by adding the statement that a primary wall may itself be pitted whenever a secondary wall is absent.

The Middle Lamella.—When a pronounced secondary wall is present the primary wall is commonly called the *middle lamella*. Formerly,

this layer was supposed to bear no direct relation to individual cells, but to be an intercellular substance, or "cement," binding them together. It is now clear that the middle lamella is not only a primary wall, but represents the fused primary walls of adjacent cells. Although this double nature is usually obscure, staining and optical effects may give evidence thereof, and it can also be seen where the wall is split by schizogenous intercellular spaces or torn apart mechanically in sectioning. The middle lamella is often thickened in the corners between the cells.

The secondary wall is built up rapidly after the inception of its development and is usually completed in a comparatively short time. In a few cases it has been reported that deposition of this layer is begun before complete cell size is attained. This is a matter, however, difficult of determination. The secondary wall constitutes the major portion of the wall of nearly all really thick-walled cells.

The tertiary wall is, like the secondary, formed rapidly. The restricted area of wall thus reinforced usually bears a definite relation to the pitting of the secondary wall, the spiral bands passing between the rows of pits, but in some instances appearing to pass over these openings.

SCULPTURE AND MODIFICATION OF THE WALL

Pits.—As increase in the thickening of the wall, especially the development of the secondary layer, takes place, thin areas are left in the wall. Such spots are known as *pits*. They are sharply defined and various in size, shape, and abundance; they are, however, constant in type in a given cell or kind of cell. The term "pit" is used to designate only small thin areas and is not applied to extensive thin areas, such as those present in protoxylem elements between the thickened rings and spirals (Fig. 46). Functionally, pits seem to be diffusion areas, regions where better interchange between cells may occur. That pits may be areas of interchange of another type also is apparent from the fact that in living cells groups of plasmodesma are frequently or always present in the pits in larger numbers than elsewhere (Fig. 12, *A, D, E*). In fact, it is possible that the presence of groups of these projections of the protoplast determines the position of pits. Pits are characteristic of all types of cells. They are, however, sometimes minute and scarce, as in some types of fibers, and are absent in some kinds of thin-walled cells.

Pit Structure and Pit Types.—A thin area in the wall of one cell is found always to lie opposite a similar one in the adjacent cell (Figs. 15; 20, *H, I, J*); the two may not, however, be of exactly the same size or shape, and frequently do not coincide exactly in position or in orientation. Oblique and unsymmetrical pits are thus sometimes formed (Figs. 16, *G*; 18, *J*). The term "pit" commonly indicates the combination of wall opposing thin areas or cavities in the wall, and also in common differs

includes the portion of the wall lying around and within the double cavity. That portion of the wall which separates the two cavities is the *closing membrane* of the pit. Where the cavities in the wall are partly enclosed by overhanging portions of the wall, the pit is said to be *bordered*, because of the border formed about the opening, or mouth, when the pit is seen in face view (Figs. 15, A, B, C; 17), in contrast with pits without such rims, which are called *simple* (Fig. 15, D, E). The bordered pit is structurally complex also in that the closing membrane possesses a thickened central portion, the *torus*, and is much thinner about the margin. The latter portion may be perforated by numerous minute

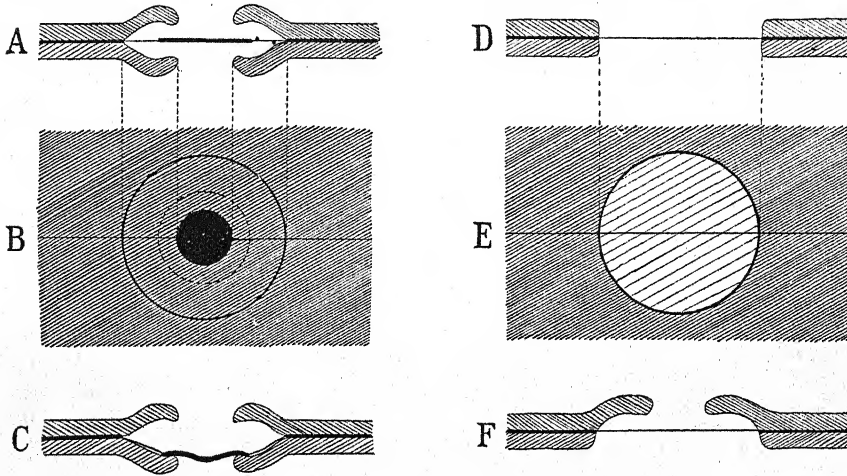


FIG. 15.—Diagrams of three kinds of pits. A, B, section and face view of bordered pit, showing the overarching borders of secondary wall which enclose the pit cavity, through the center of which passes the closing membrane whose central portion is thickened to form the torus. C, section of same showing the closing membrane in a lateral position, the torus closely appressed to the pit mouth. D, E, section and face view of a simple pit; the secondary wall does not overhang the pit cavity and the closing membrane has no torus. F, section of half-bordered pit, the secondary wall overarching in but one half of the pit. (A-C, from Sharp, after Bailey.)

openings (larger than plasmodesma openings) so that the torus is suspended by a meshwork (Fig. 16, A). The closing membrane of many bordered pits is subject to change of position within the pit cavity, such movements apparently being due to pressure changes within the cells. Thus the torus may occupy a median position (Fig. 15, A), or lie close against the opening on either side (Figs. 15, C; 16, B), seemingly functionally closing the pit, or at least greatly reducing its activities. In the lateral position it may even be distorted by the forcing of the central part against or into the opening (Fig. 16, C). The diameter of the torus is always greater than that of the opening, and hence, when the torus is in the lateral position, communication through the pit must be through the torus; when the torus is held centrally the thinner or perforated margin

provides more free, though less direct, access. Bordered pits are characteristic of water-conducting cells and of cells which are morphologically direct modifications of these. Such cells are always non-living when mature. In living cells bordered pits occur only in rare instances, as in transfusion tissue (Chap. IV). Bordered pits are perhaps best developed in the gymnosperms (Fig. 17), but occur throughout vascular plants. Simple pits are characteristic of living cells, and are found in all types of such cells, as well as in such non-living cells as have been derived in evolution directly from living cells, for example, stone cells and certain kinds of fibers. They vary much in size and shape (Fig. 19, *A, E, F, G, N*). Simple pits are not found in typical water-conducting cells. Pits lying between living cells and non-living, water-conducting cells are half-

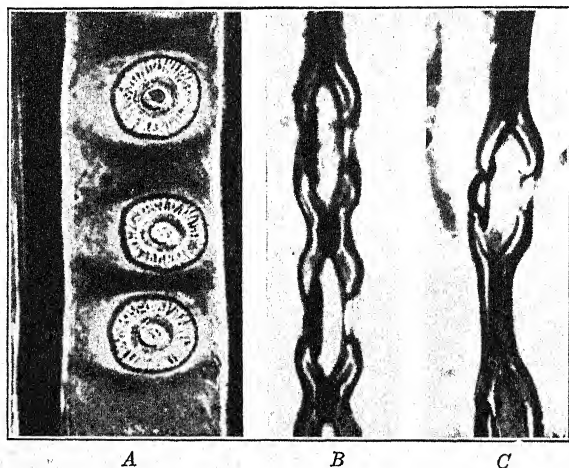


FIG. 16.—Bordered pits. *A*, in face view, showing perforations of the peripheral part of the pit membrane; *Larix laricina*. $\times 520$. *B, C*, in vertical section, showing torus in lateral position—in *C*, pressed into the pit mouth; *Pinus*, sp. $\times 1000$. (After Bailey.)

bordered (Figs. 15, *F*; 19, *B, C*; 20, *D, E*), the half on the side of the living cell being simple, and that on the side of the water-conducting cell bordered. The border is often weak, however, and a torus is poorly developed or lacking.

The bordered pit varies greatly in size and structure (Figs. 18, 19, 20). The prominent modifications of its typical form and size are those associated with the specialization and reduction of the pit as it occurs in fiber tracheids and fibers. In the typical bordered pit the cavity, which is circular in outline, is large, and the mouth, or aperture, is also circular (Figs. 17; 21, *A*). Where such pits occur in thin walls, the border may arch and bulge into the lumen, as in the spring-wood tracheids of *Larix* and species of *Pinus* (Figs. 20, *E*; 21, *B1*). Where the wall is thicker the border does not bulge and the aperture opens into a tube-like entrance and not directly into the cavity (Figs. 20, *I*; 21, *C5*). Generally, the

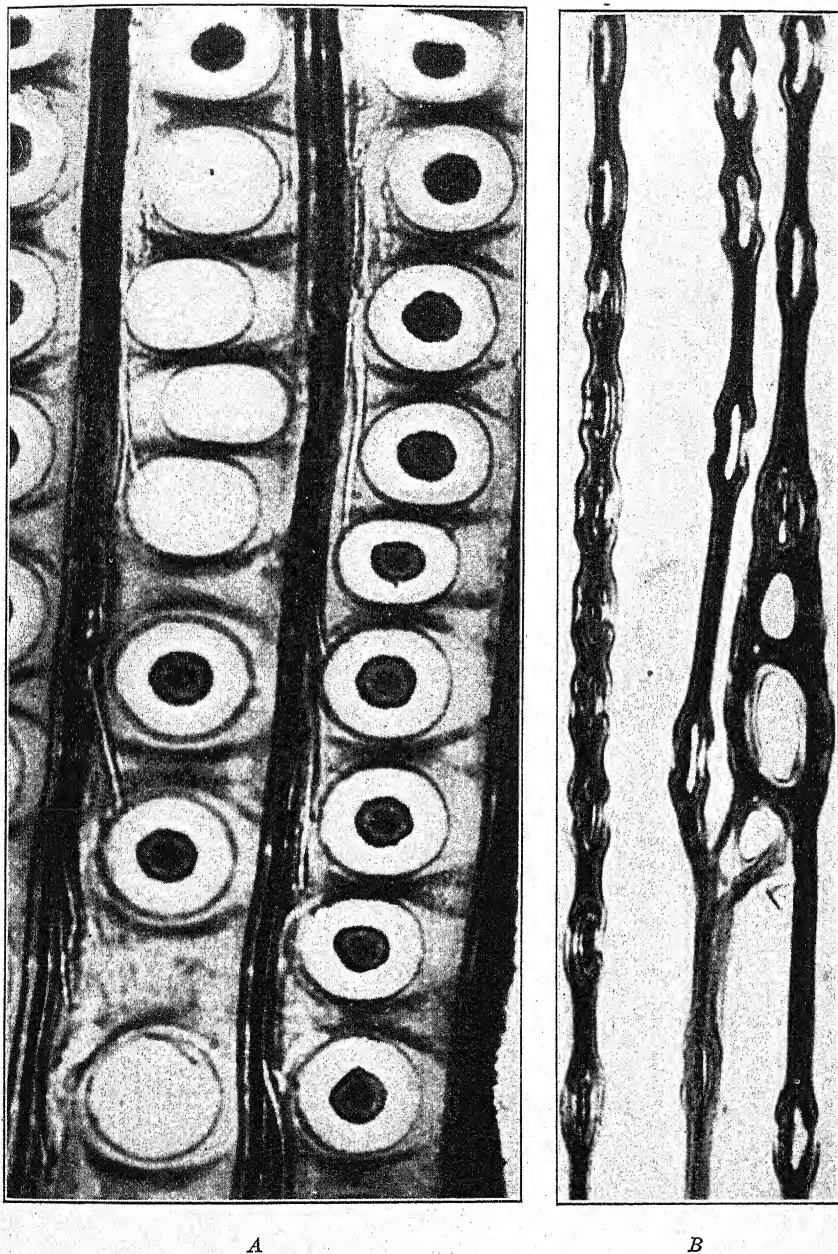


FIG. 17.—Bordered pits of coniferous wood. A, in face view. B, in section, showing border, cavity, torus, mouth. (Courtesy of the U. S. Forest Products Laboratory of Madison, Wis.)

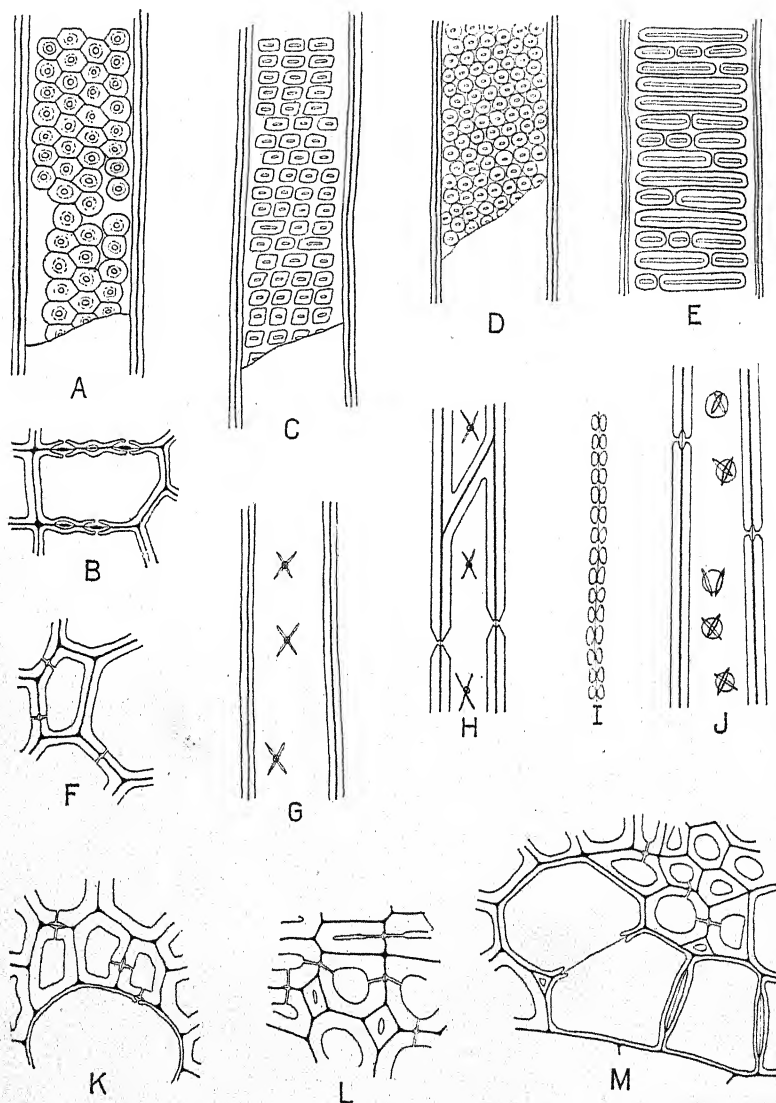


FIG. 18.—Bordered pits. A, B, crowded, angular pits in face view and in section in tracheid of *Agathis australis*. C, rectangular pits, face view, in horizontal rows in vessel of *Liriodendron*. D, crowded pits, face view, in spiral rows in vessel of *Acer rubrum*. E, elongate pits, face view, in vessel of *Magnolia acuminata*; the same pits in vertical section in I, and in transverse section in M. F, G, pits with narrow mouths, in section and face view in thick walls of wood fiber of *Populus tremuloides*. H, similar pits in wood fibers of *Magnolia*, face view and longitudinal section; the same pits in transverse section in L. J, K, pits with narrow, unsymmetrically placed mouths in wood fiber of *Pyrus Malus*, in face view and in longitudinal and transverse section. M, large, elongate pits (E) in vessels and small pits in fibers, both in transverse section in *Magnolia*.

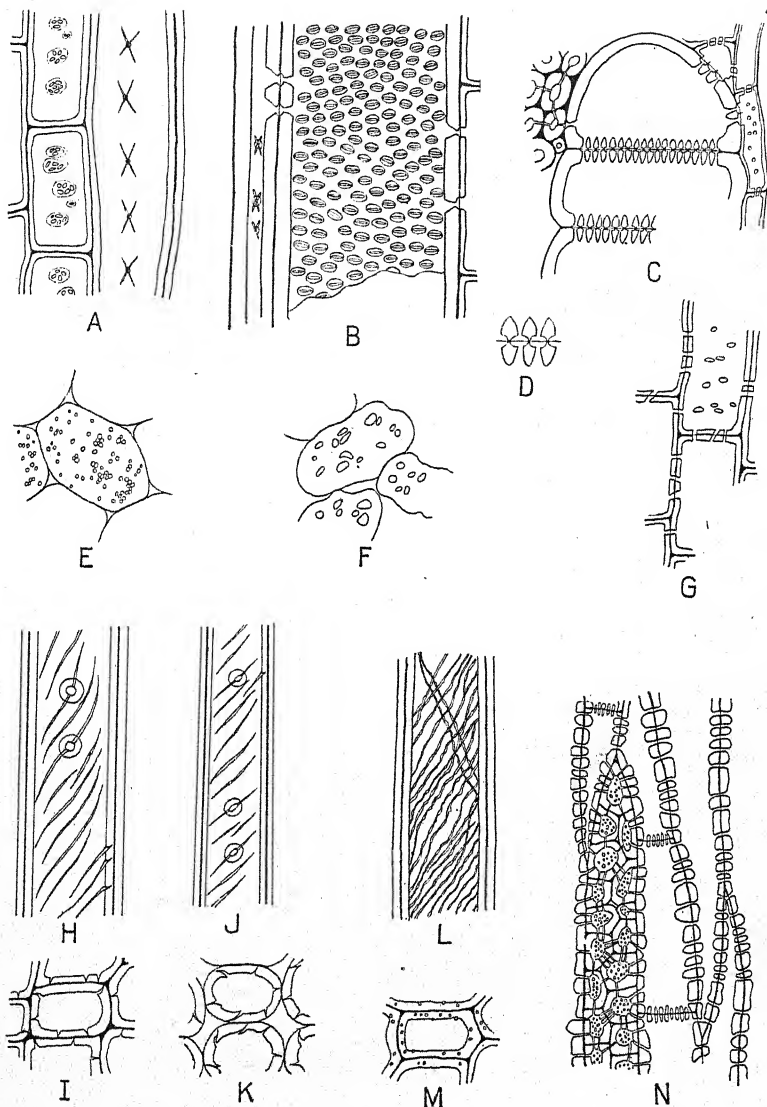


FIG. 19.—Pits and other wall sculpturing. A, clustered simple pits in wood parenchyma, and very small bordered pits in fibers, face view, in *Fraxinus americana*. B, bordered pits of two forms, face view, in vessel and in fiber, and half-bordered pits, in section, between vessel and parenchyma cell, in *Diospyros* (ebony). C, the same pits as in B, in transverse section; also simple pits, face view and section in ray and parenchyma cells. D, detail section of bordered pits between vessels, as shown in C. E and F, simple pits in thin-walled parenchyma cells—E in pith of *Chenopodium*; F, in pericarp of *Citrullus*. G, simple pits in thick-walled parenchyma of pith of *Clematis*. H and I, J and K, microscopic checking, face view and section, of secondary wall in tracheids of *Pinus Strobus* and *Sequoia sempervirens*; the cracking extends through pit mouths and simulates elongate mouths. L, M, erosion of secondary wall by fungus hyphae, simulating checking, face view and section, in tracheid of *Podocarpus*. N, simple pits in thick-walled ray cells and wood parenchyma, face view and section, in late summer wood of *Magnolia*.

thicker the wall the smaller the cavity and the smaller the aperture. In thick walls although the cavity of the pit remains always circular in outline, the apertures become narrowed and elongated, being elliptical and slit-like in outline (Fig. 21, A2-A6). When only slightly narrowed, the mouth may extend only part way to the margin of the cavity (Fig. 21, A2), or reach the very limit of the cavity (Fig. 21, A3), so that there is at that point no border. Where the aperture is much narrowed, the slit

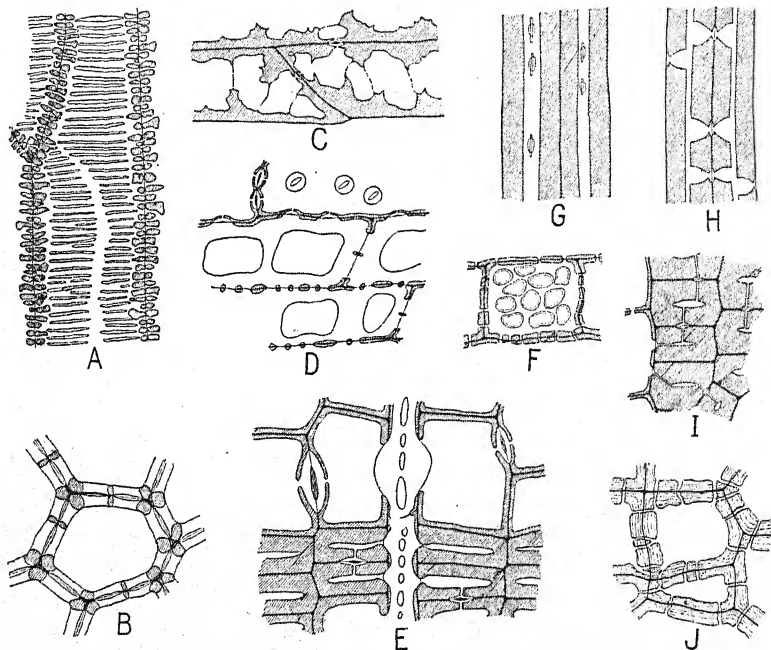


FIG. 20.—Pits. A, B, elongate bordered pits of tracheid of *Osmunda Claytoniana*, face view and section. C, bordered pits and "dentations" of wall in section in marginal ray cell of *Pinus Banksiana*. D, full-bordered, half-bordered, and simple pits, face view and section, in wood ray cells, radial section, of *Pinus Strobus*. E, similar, in part the same, pits, in face view and section, in tracheids and ray cells in transverse section of wood of *Pinus Strobus*. F, simple pits in section and half-bordered pits in face view in ray cell of wood of *Salix alba*. G, H, and I, small, narrow-mouthed bordered pits with vertical apertures coinciding in position, and with long, channel openings through the thick wall to the cavity, face view, longitudinal section, and transverse section, respectively, in wood fibers of *Eucalyptus globulus*. J, simple pits in stone cells of phloem of *Platanus*.

usually extends far beyond the limit of the cavity (Fig. 21, A4-A6); the extension of the mouth of the pit far beyond its cavity is the more extreme because the size of the pit cavity is reduced as the length of the opening is increased. These very elongate openings occur only in thick walls, and hence the channel-like entrance through the thick wall to the small inner part of the cavity is in shape like a much flattened, or laterally compressed funnel (Fig. 22). The inner opening of this funnel-like entrance remains circular. When pit mouths are circular, the two apertures lie directly opposite one another (Fig. 21, B1), coinciding in

position; when the mouths are elongate, the apertures on opposite sides of a wall are in most cases crossed, usually symmetrically (Figs. 21, A2-

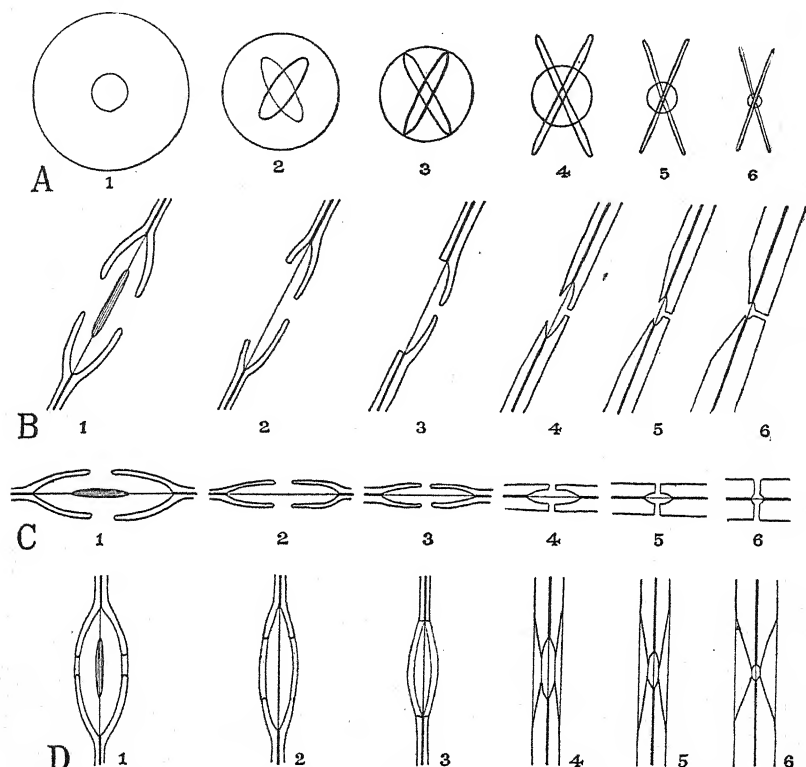


FIG. 21.—Diagrams of various types of bordered pits, showing changes of form accompanying reduction in size and function, and occurrence in walls of various thickness. *A*, face views. *B*, sections along plane of elongated mouth. *C*, transverse sections. *D*, view, "edge on," of entire pit lying in wall—the view of small pits commonly seen, because of their small size—in longitudinal sections of wood.

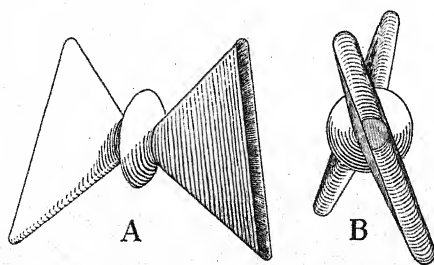


FIG. 22.—Diagram showing form of pit cavity of a bordered pit of type shown in Fig. 21, A4. The apertures are slit-like, the small cavity round in outline, the connecting channels like flattened funnels.

A6; 22). These crossed pit mouths are conspicuous features of pit marking in the walls of wood cells (Figs. 18, *G*, *H*, *J*; 19, *A*, *B*). The pit

cavity in such cases is complicated in form (Fig. 22). With extreme reduction the borders of the pits disappear, and slit-like pits, essentially simple in structure, are formed (Fig. 21, A6, C6). Morphologically, such pits are, however, clearly bordered pits. The pits of libriform wood fibers are often wholly vestigial, being hardly more than markings on the wall. In much reduced pits the closing membrane is of simpler structure, the torus being lacking, and the capacity of the membrane to change its position being lost. Such pits are probably physiologically functionless or nearly so.

Other Wall Sculpturing.—The irregular modeling of the inner surface of the cell wall is in large measure due to the presence of pits. Pits and the perforations of the walls of vessels (Fig. 35) form conspicuous structural modifications. Even more prominent are the secondary wall thickenings in the form of rings, spirals, and reticulations which are characteristic chiefly of protoxylem (Figs. 46, 47). External sculpture is

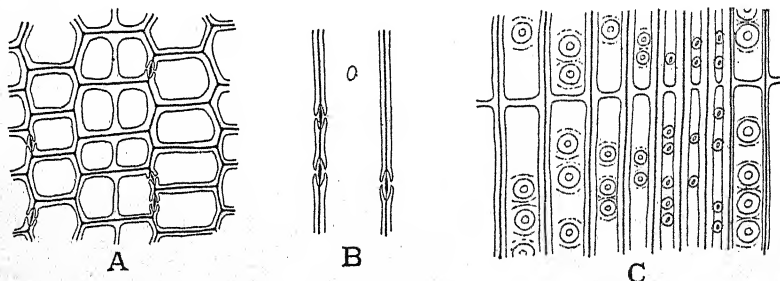


FIG. 23.—Trabeculae in the tracheids of *Abies balsamea*. A, transverse section. B tangential section. C, radial section.

less commonly conspicuous, and is found as nodules, flutings, grooves, and pegs in pollen grains and spores, in the free wall of epidermal cells, especially those of floral parts and fruits (Figs. 131, A; 132, F). Internal projections in the form of bars, ridges, and reticulations are occasional, for example, the "dentations"—really ridges—of the ray tracheids of hard pines (Fig. 20, C), the *trabeculae* of tracheids (Fig. 23), the septa of septate fibers (Fig. 34, D), and the thickening or supporting rods and meshes of velamen cells and of other similar cells.

The Chemical Nature of the Cell Wall.—The wall of the plant cell is composed fundamentally of carbohydrates of the cellulose group. When first formed the wall is of pectose or of some closely similar carbohydrate; this substance is characteristic of the primary wall until full cell size is attained. Later, the wall substance becomes more firm and hard, insoluble pectates, especially pectate of calcium, being formed. The secondary wall is laid down as a layer of pectose and cellulose, and the tertiary as a layer of cellulose. Both of these inner wall layers, however, are usually changed immediately and rapidly by lignification. The

latter process is complex chemically, in that "lignin" itself consists of a group of substances, the nature of which is not fully known. The composition and the specific gravity of lignin (and of lignified walls) seem to be fairly constant, as are also its staining reactions. As a result of the modification of cellulose and pectose walls, mucilaginous walls may be formed. Merely the innermost layer may be affected in this way, or the entire wall may be transformed. Under extreme conditions, including those which are degenerative or pathological, the walls may break down entirely and cellular structure be lost, as is the condition in *gummosis*. Mucilaginous walls serve many quite different functions—water storage, food storage, and various minor functions associated largely with seed and fruit coats and with fruit pulp. The function of mucilaginous walls in wood fibers, such as those of the black locust and red oak, is not fully understood.

Cutinization and *suberization* result from changes involving certain waxy or fatty substances, chiefly cutin and suberin, respectively. These changes are waterproofing, since they provide layers strongly impervious to the passage of water (which penetrates cellulose and lignified walls freely).

Mineralization, the infiltration by, or deposition of, inorganic salts in the wall, is only rarely a prominent feature of wall nature. All mature walls, however, contain small amounts of mineral matter, sometimes in the form of embedded crystals; the latter, however, are rarely seen. Silica, and oxalate and carbonate of calcium occur most abundantly. The walls of the outer cells of the stems of horsetails, grasses, sedges, and some other plants contain high percentages of silica. Where mineralization is restricted to small areas in the wall and is extreme, projections known as *cystoliths* are formed. These distorted portions of the wall take various shapes; they are clearly distinct from inorganic material lying in the protoplast or in the lumen. Cystoliths are characteristic of a few families, such as the Urticaceae and Moraceae, and of some smaller groups, but are not common or important features of cell structure.

Chitinization, infiltration by chitin, occurs probably only in the lower plants, in certain algae and fungi especially.

Other changes in the wall involve resins, gums, oils, tannins, and tannin-decomposition products, various aromatic and coloring substances, and many others of minor importance. Tannin is important in relation to durability, and it and other substances are responsible to a large extent for the durable and useful qualities of certain woods, and of heartwood (Chap. VII) as contrasted with sapwood. These substances are present not only in the walls, but often fill the lumina and pit cavities as well. They are formed in part from the contents of the living cells of the immediate region, but doubtless also in part from additional material brought to the region.

The modifications discussed above may involve all three of the chief layers of the wall or any of these alone. However, the primary wall is usually less changed than are the other parts. In the lignification of a cell, for example, the primary wall may be to some extent changed into "lignin," but to a less degree than is the secondary wall.

All these changes are in nature either those of direct chemical transformation or molecular replacement; or those of apparent change brought about by infiltration, or by deposition of large amounts of new, different substances, within the original wall, so adulterating the latter that the first substance is obscured. Pseudo-changes are secured by the addition of new material in lamellae over the old wall, completely burying the latter. Such modifications may accompany the maturation of the wall in cell ontogeny, or may take place long after cell maturity, for example, when sapwood becomes heartwood, and when cortical photosynthetic parenchyma cells or phloem conducting parenchyma cells become stone cells after a long period of activity in their first condition.

THE CUTICLE

Over most of the surface of the aerial parts of vascular plants there is a layer of a waxy substance, *cutin*. This constitutes the *cuticle*, a coat which serves to protect the underlying cells from too rapid loss of water. The cuticle is structureless and covers the epidermis as a whole, following the contour of the cells much as a heavy coat of paint covers a shingled wall (Figs. 24, 135). Growing points lack this layer and some ephemeral organs such as stamens have so thin a coating that it is not readily detectable. A thin cuticle is present sometimes even on the inner epidermis of the ovary, and on the integuments of the ovules, as in the Amaryllidaceae. Roots and the entire body of submersed plants have no cuticle. The cuticle is a continuous layer, the only breaks in its continuity being those due to the presence of stomata and, in older stems, of lenticels.

Origin and Structure of the Cuticle.—In origin the cuticle is probably a secretion of the protoplast of the epidermal cells, the secretion being passed through the wall in some manner not understood. In some cases, pits and plasmodesma have been reported on the outer epidermal walls and the suggestion made that cutin is passed through these; but such thin spots or perforations if they exist at all are apparently very rare. It has also been stated that the cuticle is a transformed outer layer of the cell wall, but this is improbable.

The surface of the cuticle is smooth, or in some cases is roughened by irregular cracks, thickenings, or slight ridges. Many so-called *cuticular pegs* and *ridges* are projections of the epidermal cells coated by the cuticle (Fig. 24, G). The flutings or striations of epidermal papillae lie in the cell wall itself. Minute particles of wax, lying on the surface

of the cuticle, are the cause of the glaucous character of stems and leaves, and constitute the "bloom" of fruits. Wax also occurs in larger particles, as on the fruits of the bayberry, *Myrica*, and even entirely coats the leaf in the wax palm, *Copernicia*. The thick cuticles of fruits are present only on mature fruits, developing rapidly as mature size is

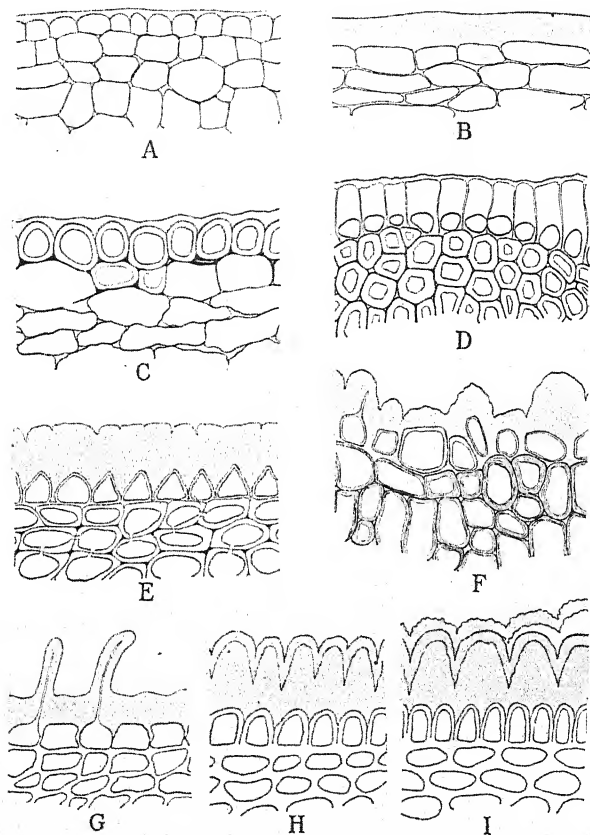


FIG. 24.—The cuticle. Sections of the epidermis and adjacent tissues, showing various degrees of thickness and of extent of the cuticle between epidermal cells. (For thin cuticles see Figs. 132, *B*; 134, *A*, *C*; very thin cuticles are not illustrated.) *A*, *Citrus sinensis* (orange), fruit. *B*, *Pyrus Malus* (var. Ben Davis), fruit. *C*, *Dracaena Goldieana*, stem. *D*, *Dasyllirion serratifolium*, leaf. *E*, *Acer pennsylvanicum*, stem, the older, outer layer cracking and disintegrating. *F*, *Smilax rotundifolia*, stem. *G*, *Vaccinium corymbosum*, stem. *H* and *I*, *Cornus circinalis*, stem, showing two stages, the outer, older layers being replaced by new ones formed below.

approached or attained; but in some stems with thick cuticles the layers must be accommodated to considerable increase in stem diameter when the epidermis persists for several years. In such plants as these—for example, in species of *Acer*, *Cornus*, *Viburnum*, and *Kerria*—the original cuticular layer is cracked or ruptured and the break is repaired by the

secretion of new material from beneath, or an entire new layer is formed (Fig. 24, *H, I*).

The thickness of the cuticle varies greatly (Chap. XIV), plants of shade and of moist habitats having thin cuticles and those of dry, sunny situations generally having thick cuticles. Many fruits, such as the apple (Fig. 24, *B*), plum, tomato, and persimmon, when ripe, have a firm, thick cuticle. This conserves the water in the fruit after a renewed supply is no longer available. An example of the effectiveness of this is seen in the fact that in the drying of prunes the cuticle is commonly weakened or removed. To the presence of a heavy cuticle is due, in part, some of the keeping qualities of fruits.

Functionally, the cuticle is sometimes reinforced by a condition of *cutinization*—infiltration by cutin—of the walls of the epidermal cells, and, in extreme cases, of the subepidermal cells also. The cutinization may involve only the outer walls of the epidermal cells or the outer and also the lateral walls; the inner walls are rarely involved in the process. Cutinization is a process different from *cuticularization*, the formation of a cuticle.

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CHAPTER III

MERISTEMS

Growth in an organism consists fundamentally of increase in the size of the protoplasmic body. Closely associated with such increase in size is differentiation; in fact, differentiation is often thought of as a phase of growth. In some plants, especially the more primitive forms, growth may take place without the partition of the protoplasmic mass into cellular units; in cellular plants, however, any considerable amount of growth is manifested by cell division and the subsequent enlargement of the derivative cells. In plants with little or no tissue specialization, cell division may occur throughout the plant body or in any region thereof, thus increasing the mass of the plant body. In plants with specialized tissues, on the other hand, growth and the formation of new cells are localized in certain more or less definite regions known as *meristems*. The cells of these regions are called *meristematic cells*, and together these cells form *meristematic tissue*.

Meristematic and Permanent Tissues.—Meristematic cells, tissues, and regions, therefore, are those in which cell division is still going on and which are not yet fully differentiated. When such cells and tissues have become fully differentiated and mature, they are said to be *permanent*. There are, then, two kinds of cells and two kinds of tissues from the standpoint of stage of development—meristematic and permanent. Permanent cells, however, are not necessarily permanent in the usual sense of the word, since they may change both in form and in function after a longer or a shorter period of existence as completely differentiated, or mature, cells. For example, epidermal cells or typical cortical cells may form a cork cambium months after those parts of the stem in which they lie become mature; similarly, photosynthetic cells of the cortex and parenchyma cells of the older phloem may become stone cells. Thus, cells may change their nature markedly a long time after becoming mature; they may again become active in division, forming other cells and even meristems. Many kinds of living cells which have walls that are not extremely thick or otherwise highly specialized may in this way become meristematic.

Meristematic tissues have certain characteristic features not common to permanent tissues. In general, meristematic tissues are made up of cells with their diameters essentially alike; their walls thin and homogeneous, usually without evident pits; the protoplasm abundant and active;

the nuclei large; the vacuoles small or lacking; and intercellular spaces absent (Figs. 6, A; 25; 28). The cambium, however, is a meristematic tissue which in some ways does not fall under this description.

CLASSIFICATION OF MERISTEMS

Promeristem.—The youngest cells in a region of a growing plant body in which the formation of new organs or parts of organs is taking place constitute a *promeristem*, or *primordial meristem*. Here the foundation of all organs is laid down. The promeristem is of rather limited extent, varying in different plants, and is not definitely set off from the older meristematic tissue into which it merges. For example, there is at the tip of the stem a growing region of some length; only the youngest part of this, the apical portion, is promeristem (Figs. 25, 42). Promeristem represents, then, a very early stage in development. Later, promeristems gradually become differentiated; first, into partially developed tissues (older meristems), where the beginnings of specialized structure are present, but in which cell division is still going on; after this, into mature tissues. For the partly developed tissues in which the formation of new cells is still taking place to some extent no satisfactory distinguishing term exists, though meristems at this stage are often called "histogens" (p. 47).

Primary Meristems.—Meristems such as those which build up the fundamental structure of the plant and which are derived directly from the promeristem are *primary meristems*. Such tissues have retained their meristematic characteristics from their beginning in the promeristem, and, in fact, are merely a later stage in the development of the promeristem. The entire apical growing region, including the promeristem, is sometimes known as a primary meristem. Thus the promeristem may be considered as a part of primary meristem, or as the early stage of primary meristem. The cambium (with some exceptions) is a primary meristem, since it is derived directly from promeristem without the tissues involved losing their meristematic characteristics at any time; this meristem is not, however, concerned with the formation of the fundamental body structure.

Primary meristems fall into two distinct groups: those in which cell division takes place in three or more planes, such as that which occurs in the tips of axes; and those in which the new tissue is produced by the consecutive division of a given group of cells, dividing largely in one plane only, a condition found in the cambium. In the former a cylindrical body is divided into numerous cells by divisions transverse and longitudinal to the axis and also in many other planes; in the latter, division of the cambium cells is chiefly in a plane tangential to the xylem cylinder.

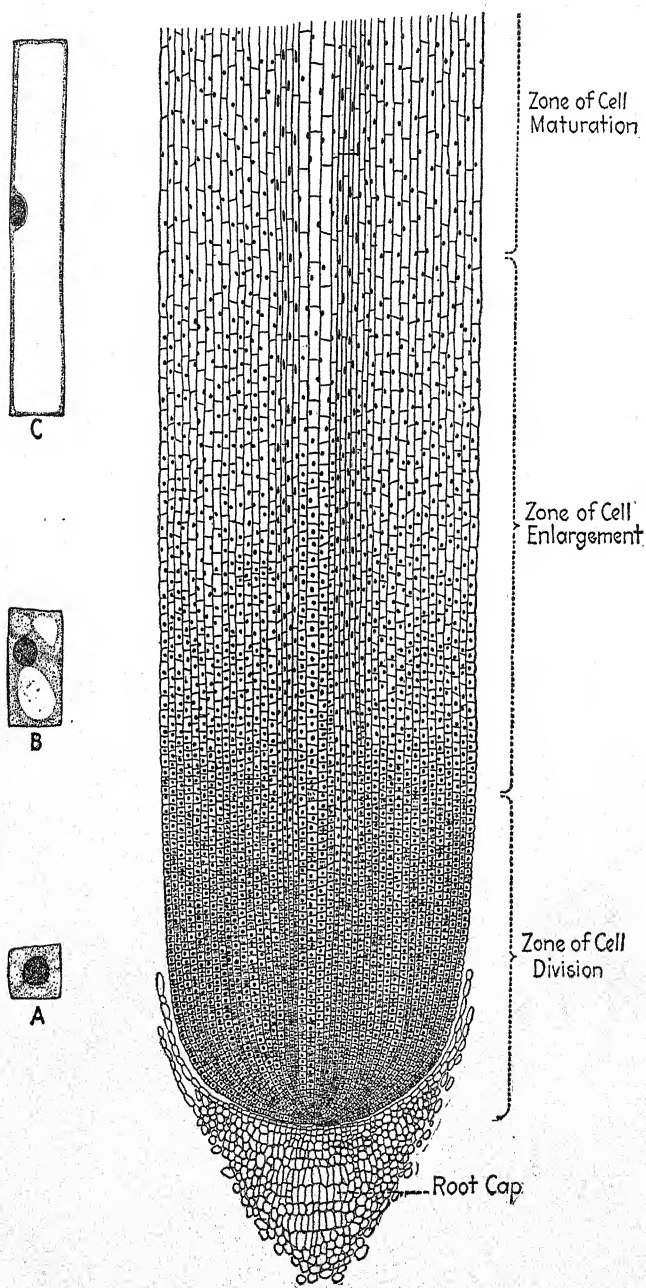


FIG. 25.—Longitudinal section of a growing root tip. In the apical portion, or zone of cell division, the tissue is promeristem; here the cells are small, rich in cytoplasm, with large nuclei, and without vacuoles, *A*. Behind the promeristem is the zone of cell enlargement; here the cells are rapidly elongating and vacuoles appear in the cytoplasm, *B*. Behind this region is the zone of cell maturation; here the cells are beginning to assume mature characteristics of size, shape and structure; a large vacuole occupies the center of the cell, restricting the cytoplasm to the peripheral region. Of the zone of cell maturation only a small part is shown. All of the tissue illustrated (except the root cap) is meristematic, at least in part. (After Sinnott.)

Secondary Meristems.—*Secondary meristems* are of markedly different origin in that they always arise in permanent tissues. The cork cambium, for example, is a secondary meristem, since it is formed from mature cells—cortical, epidermal, or phloem cells, or, in fact, from any living cells which do not have a thick, rigid wall. Thus, when wounding

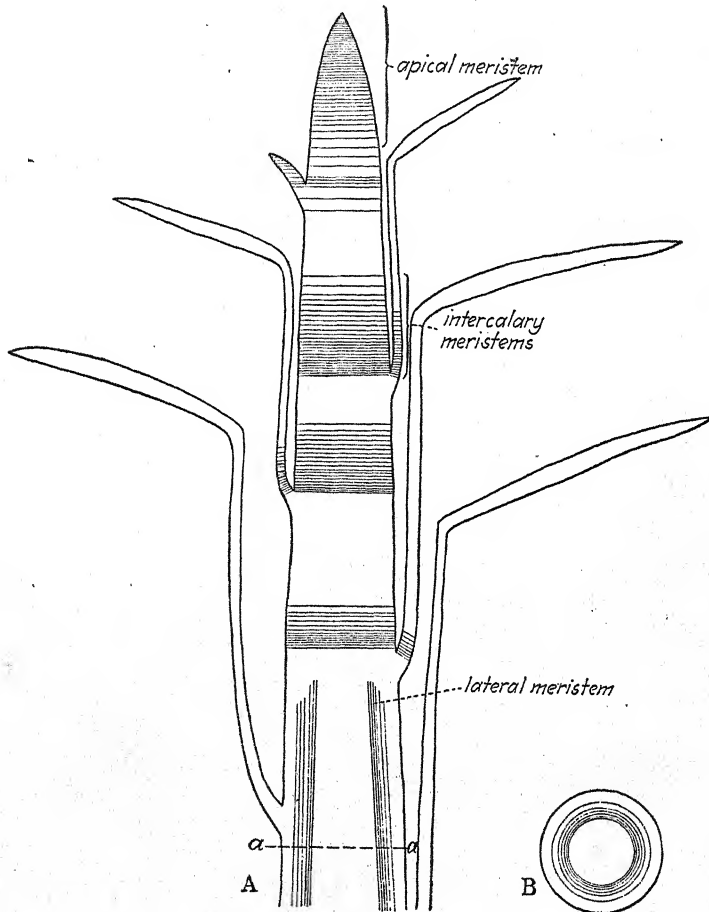


FIG. 26.—Diagram to show position of meristems. The closely lined areas are youngest; the unlined areas are mature or slowly growing. A, longitudinal view. B, cross section of A, at level a-a.

occurs, cells adjacent to the injured cells, which are mature in every way, may again become meristematic and divide to form a functioning cork cambium. As compared with primary meristems, secondary meristems are of infrequent occurrence and of minor importance, the cork cambium being the outstanding example.

Classification of Meristems on the Basis of Position.—On a basis of position in the plant body, meristems are classified as *apical*, *intercalary*,

and *lateral*. Apical meristems are those which lie at or close to the apices of the axis and of the appendages, and are commonly called *growing points* (Figs. 27, 28). Intercalary meristems are those which lie between regions of permanent tissue, as, for example, at the base of the leaves of many monocotyledons (Fig. 26). Lateral meristems, as the name implies, are situated laterally in an organ (Fig. 26). The cambium and the cork cambium are lateral meristems.

Apical Meristems.—Apical meristems, or growing points, occur universally at the tips of the roots and stems of vascular plants. By their activity increase in the length of the axis is accomplished and the primary structure of the plant laid down. In such meristems the pro-

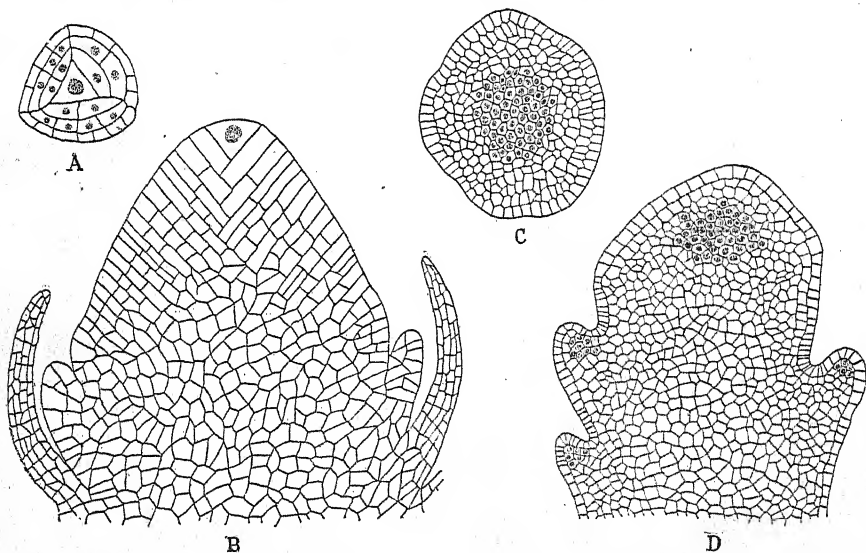


FIG. 27.—Apical cells. A, B, the stem tip of *Equisetum* in transverse and longitudinal section, showing the solitary, terminal apical cell, and the derivation of cells therefrom. C, D, stem tip (winter bud) of *Vitis* in transverse and longitudinal section, showing group of subterminal apical cells (the number indefinite and difficult of determination).

meristem is located at the apex of the growing point, the initiating cells being terminal or subterminal.

Apical Cells.—In general, apical promeristems fall into two classes: those which have their origin in a single cell and those which are formed from a group of few cells. Those originating or initiating cells which maintain their individuality and their position at the apex are called *apical cells*, or *apical initials*.¹ Among vascular plants solitary apical cells occur in the majority of ferns, in the horsetails, and in a few other pteridophytes (Fig. 27, A, B). They have been reported in the gymno-

¹ The term "initials" is used in histology to indicate any cells which by continued division form many new cells, maintaining their own individuality and meristematic condition.

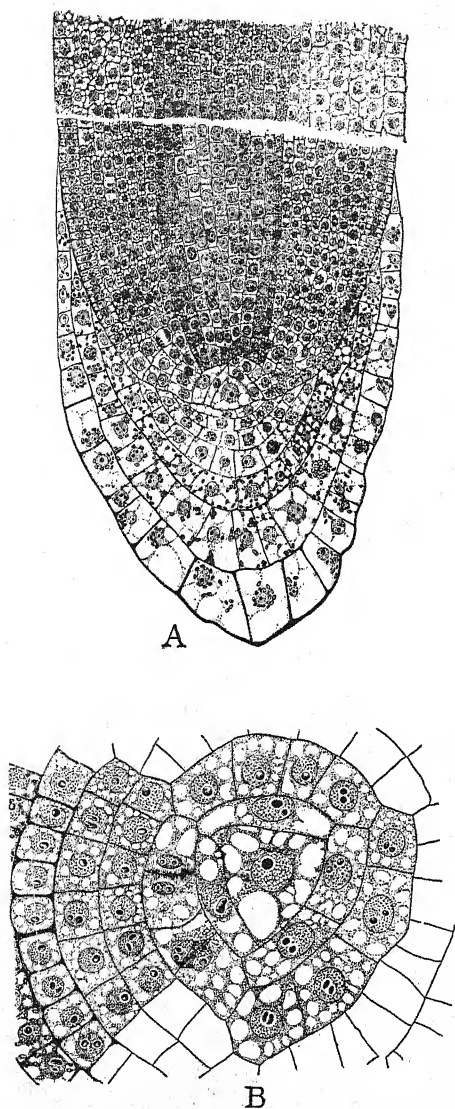


FIG. 28.—Root tip of *Pteris*. A, median longitudinal section, showing apical cell with four "cutting faces" (one not in plane of section), and the development of tissues from this cell, especially the root cap. Plerome, periblem, and dermatogen are differentiated. B, transverse section through apical cell, showing the three faces from which cells are cut off to form the root proper. (After Hof.)

sperms, but the number of apical cells in this group is in doubt. The monocotyledons and a few of the lower dicotyledons are said to have two or three apical cells, all other angiosperms having several to many (Fig. 27, *C, D*). The determination of the initiating cells in the seed plants is difficult.

Types of Apical Cells.—In the plants which have solitary apical cells several types are distinguished by shape and by the number of sides from which new cells are cut off. The two most common are the lenticular, or two-sided, cell (not found in vascular plants) and the pyramidal, or three-sided, cell (Figs. 27, *A, B*; 28). The former is, in shape, strictly a three-sided cell and the latter a four-sided cell, but new cells are formed only from two and three sides respectively; hence terms which apply to the activity of the cell rather than to its shape have been given. The side from which no new cells are formed lies in the direction of growth. In roots where root caps are present cells are cut off on this face also (Fig. 28). The size of the apical cell is reduced only temporarily by the formation of daughter cells and its position is maintained indefinitely.

(The behavior of apical cells in segmentation, and of the cells which are cut off by the apical cells, is of importance in the study of the morphology, both vegetative and reproductive, of the bryophytes.) Cells in certain positions and of certain origin always form the same tissues or organs. It was formerly held that this must also be true in general of vascular plants, but such is clearly not the case. The behavior of a given segment of an apical meristem is usually without morphological significance in the groups of plants above the bryophytes.

Intercalary Meristems.—Intercalary meristems are, in reality, only a type of apical meristems, since they are parts of such meristems which have become separated from the apex by permanent tissues and left behind as the apical meristem moves on in growth (Fig. 26). For example, there is an intercalary meristem at the base of the internode in the horsetails and in many grasses, just below the node in some mints, and at the base of the leaf in some plants, as in *Pinus* and *Iris*. The function of intercalary meristems, in common with that of apical meristems, is to increase the axis or the organ in length and to lay down the fundamental primary structures. In meristems of this type the promeristem may be basal (Fig. 26), median, or uppermost in position relative to the older parts of the meristem. Generally, intercalary meristems function slowly and ultimately disappear, being wholly transformed into permanent tissues.

Lateral Meristems.—Lateral meristems are composed of initials which divide for the most part in one plane only and provide for the constant renewal of certain important tissues with a consequent increase in the diameter of the axis or organ concerned. The cambium is by far the most important meristem of this type. It is ordinarily a cylinder of

initial cells completely surrounding the xylem core of a woody axis and forms new tissues by tangential division. The radial and transverse divisions which occur provide for the increase in the circumference of the meristematic layer itself (Chap. VI). The cambium has sometimes been called "*the lateral meristem*," but phellogen layers should also be considered as belonging in this class.

Early Differentiation of Meristems.—Behind the apical promeristem—or in many intercalary meristems in front of the promeristem—in what may be called the general meristematic region, there is gradual differentiation, which becomes progressively greater and greater from the promeristem toward the region of completely mature primary tissues, that is, in older and older tissues. The progress of this differentiation sooner or later may render evident certain more or less distinct regions which have been designated *histogens*. In many plants differences in cell size and shape, in cell contents, and in arrangement of cells, set off a central core, or region, known as the *plerome*, and an outer limiting layer, epidermis-like, the *dermatogen*. The part lying between these is the *periblem* (Figs. 28, A; 29). These three parts of the developing axis are also sometimes called *the primary meristems*; however, it seems better to consider them as merely sections or regions of primary meristem.

The differentiation of developing portions of an axis into plerome, periblem, and dermatogen does not occur in all plants, and when present varies much in distinctness. When these differentiated regions are present they have apparently little or no physiological or morphological significance; therefore, these terms are becoming less and less used. For convenience in designating regions, they may, however, be retained.

It is chiefly because of this lack of uniformity in occurrence and in morphological significance that the distinction of these regions is of little value. The plerome and dermatogen are more prominent in roots than in stems. The plerome may be distinct nearly to the apex and the dermatogen may form a layer apparently completely encasing the axis

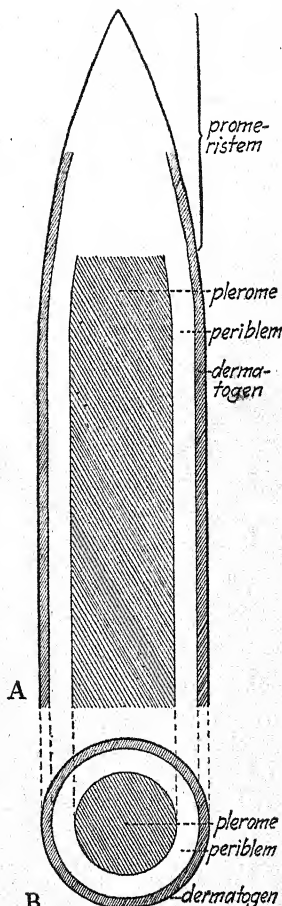


FIG. 29.—Diagram of axis tip to show "histogen" regions. A, longitudinal section. B, transverse section.

tip, or the entire terminal portion for some distance may consist of a mass of uniform isodiametric cells. Certain members of a group of apical cells may form the plerome, and others the periblem and dermatogen, or all cells may seem to take part in the formation of each of these layers. In development the plerome usually becomes the entire central cylinder; but it may form the pith alone, or the pith and vascular tissues without the pericycle. The periblem usually forms the cortex, but not infrequently the pericycle and vascular tissues also. A dermatogen is in most cases formed very early by tangential divisions in the outer cells of the promeristem (Fig. 28, A). Later divisions in this area are all anticlinal (at right angles to the surface), but otherwise may be in any plane. However, in the clubmosses and rarely in other vascular plants the dermatogen is formed from the periblem relatively late, and not by a uniform series of periclinal divisions.

Another series of terms, chiefly physiological in significance, has also been used for these regions. The name *protoderm* is given to the dermatogen and the term *procambium* is applied to that part of the plerome which, at early stages, possesses elongate, tapering cells. In this usage the term "procambium" is applied only to those groups of elongate cells, distinct because of their shape, which later form conducting and fiber cells and also other surrounding cells of a different type, such as photosynthetic parenchyma; it is not synonymous with the morphological term *procambium*, which indicates the early stage of morphological vascular units (Chap. V). The remainder of the axis, that is, the periblem and parts of the plerome, under this classification is called *fundamental meristem* or *ground meristem*. Parenchymatous tissues and sometimes those of other types developing from this meristem are loosely termed *fundamental tissues*, *ground tissues*, and *fundamental parenchyma*. Together they form the *fundamental tissue system*, though the latter term may be applied to the cortex alone. This group of terms forms a sort of "catch-all" for tissues or regions of less markedly specialized function. The series of terms is as a whole very indefinite in meaning and usage, and consequently is of much less value than the preceding series.

Further discussion of the meristematic development of tissues and organs will be found under the treatment of these structures in Chaps. V, X, XI, and XII.

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CHAPTER IV

TISSUES

There is among the individual cells of some of the less specialized thallophytes very little or no "division of labor." In such plants the cells are not usually various in size, elaborate in shape, or complex in arrangement; only simple vegetative cells and reproductive cells are present. The cells which are alike in structure and function form a group or mass which can be called a *tissue*. Thus, a group of vegetative cells is a *vegetative tissue*, and, similarly, a group of reproductive cells is a *reproductive tissue*. Here similarity of structure and function binds certain cells together as a tissue. In the higher plants more complex tissues require, however, a more comprehensive definition. A tissue may be said to be a continuous organized mass of cells, usually similar in origin, and essentially alike in form and general function. Such a definition is loose, but one more restrictive is difficult to make and to use. From the physiological viewpoint function by itself may bind cells together; similarity of origin, and even continuity, are not essential. Thus widely scattered cells may form a tissue. From a morphological viewpoint, continuity and similarity of origin are of first importance. Clearly, the two uses of the term are distinct.

Classification of Tissues.—Tissues are classified in many different ways—on the basis of form, function, structure, method or place of origin, stage of development, etc.

Parenchyma.—Simple vegetative tissue, that is, tissue which is not complex or elaborate in structure or form, like that which makes up the body mass of lower plants, and the non-specialized portions in more complex plants, is called *parenchyma*. Parenchyma is a rather loosely used term in that it is applied to all generally unspecialized and fairly simple tissues which are concerned largely with the ordinary vegetative activities of a plant. Parenchyma is, obviously, phylogenetically the primitive tissue, since the lower plants have undoubtedly given rise to the higher plants through specialization, and since the single type or the few types of cells found in the lower plants have become by specialization the many and elaborate types of the higher plants. Further, all meristematic tissue is unspecialized. Hence, it is parenchyma-like—in fact, is often called parenchyma—so it can be said that, ontogenetically also, parenchyma is the primitive tissue. Thus, for the classification of tissues, a foundation is given by the determination of the tissue of which all others are modifications.

Parenchyma and Prosenchyma.—A tissue type set off on form and function is that known as *prosenchyma*. Prosenchyma is made up of elongate, pointed cells which are concerned less with the simple vegetative activities of a plant than with the specialized functions of support, protection, and conduction. All tissues may be separated into parenchyma and prosenchyma, but such a classification is not seen in recent writing. It is practically obsolete, but the term "prosenchymatous" is often used to describe cells which are elongate and taper-pointed. Parenchyma cells are thin-walled; with diameters nearly alike, with protoplasmic contents usually present; prosenchyma cells are thick-walled and elongate, with pointed ends, with protoplasm small in amount, or wanting. However, parenchyma cells are often thick-walled and elongate, and in age with little or no protoplasm; and prosenchyma is occasionally thin-walled, and even more often possesses protoplasts. No distinctive character is left, therefore, but the pointed end, so that the classification is weak and practically useless; hence it has passed out of use.

Stereome and Mestome.—From the standpoint of function, tissues may be classed as those which are chiefly supporting and protecting, and those which are chiefly conducting and "packing." The supporting and protecting cells are known collectively as *stereome*, the hard tissue; the conducting and packing tissues as the *mestome*. This classification is based on function alone, and is found only in physiological texts. In this, as in nearly all classifications, many tissues fall definitely into neither group; they are partly supporting and partly conducting. Therefore, no sharp line can be drawn between these two types of tissue. The mestome is further divided into the *hadrome*, that which conducts water and substances absorbed with water; and the *leptome*, that which conducts the food of the plant. These terms are not synonymous, however, with xylem and phloem, respectively, as morphologically used. They are synonymous with these terms as often used by physiologists. Hadrome and leptome include only those cells of xylem and phloem which are concerned directly with conduction. All supporting cells, such as fibers and stone cells, are part of the stereome. The terms "stereome," "mestome," "hadrome," and "leptome" are physiological terms. They have little use except in the description of structure in terms of function alone, and have not been adopted to any extent.

Primary and Secondary Tissues.—Another classification, based on method of development, is the most generally useful classification of tissues and one which is necessary to an understanding of the structure of the plant body morphologically or histologically. On this basis, tissues are either *primary* or *secondary*. Those tissues which are formed by primary meristems of the first type are *primary tissues*; that is, they are those which are developed directly or indirectly at the growing points by cell division in several or many planes (Chap. III). Tissues which are

formed by primary meristems of the second type, such as the cambium, and those which are formed by secondary meristems, are *secondary tissues*. These tissues are formed largely by cell division in a single plane, individual cells consecutively forming many new cells, which, because of this method of formation, lie in definite rows. These are then two quite different types of tissues, different in their method of origin, and different in the structural arrangement of the cells composing them.

Cells have already been classified on the basis of their stage of development as meristematic and permanent; the same terms with similar meanings are also applied to tissues.

Simple and Complex Tissues.—In specialization from meristem, changes in the shape, structure, and nature of the cell wall and of the protoplast produce various cell types. Some of these types are associated only with certain restricted tissues or organs, as, for instance, tracheids with xylem, and cork cells with phellem. Other cell types may be found anywhere throughout the plant body, either singly or in masses of various size. Where cells of a single type occur together in a uniform or homogeneous mass, the tissue thus formed is *simple*. When cells of more than one type are associated in a tissue, the tissue is *complex*. Only a few of the many cell types which are present in plants form simple tissues, and some of these same cell types, such as parenchyma and sclerenchyma, are common constituents of complex tissues.

THE COMMON SIMPLE TISSUES

The simple tissues which are most common in plant bodies are *parenchyma*, *sclerenchyma*, and *collenchyma*. These terms are names of tissue types, but are also applied to cells; for example, a certain cell may be called "a parenchyma cell." Such a cell is either a unit of the simple tissue, parenchyma, or is a parenchymatous cell in a complex tissue. The adjectives, parenchymatous and sclerenchymatous, indicate cells which possess some of the characteristics of the cells of parenchyma and of sclerenchyma, respectively, but which may not belong definitely in those tissues. There are thus parenchymatous fibers, sclerenchymatous cork cells, etc.

Parenchyma.—The general characters of *parenchyma* are: diameters essentially equal, walls thin, protoplasm present and active, and a capability for cell division even when the cells are permanent cells (Figs. 30; 39). Parenchyma makes up large parts of various organs in many plants. Pith, the mesophyll of leaves, the pulp of fruits, consist chiefly of parenchyma; the cortex and pericycle are often wholly or in large part parenchyma, and parenchyma cells occur freely in xylem and phloem. Because in parenchyma there are embedded, and out of parenchyma, as meristem, there develop other more specialized cells, tissues, and tissue systems, parenchyma has been called *ground tissue* and *fundamental tissue*. These

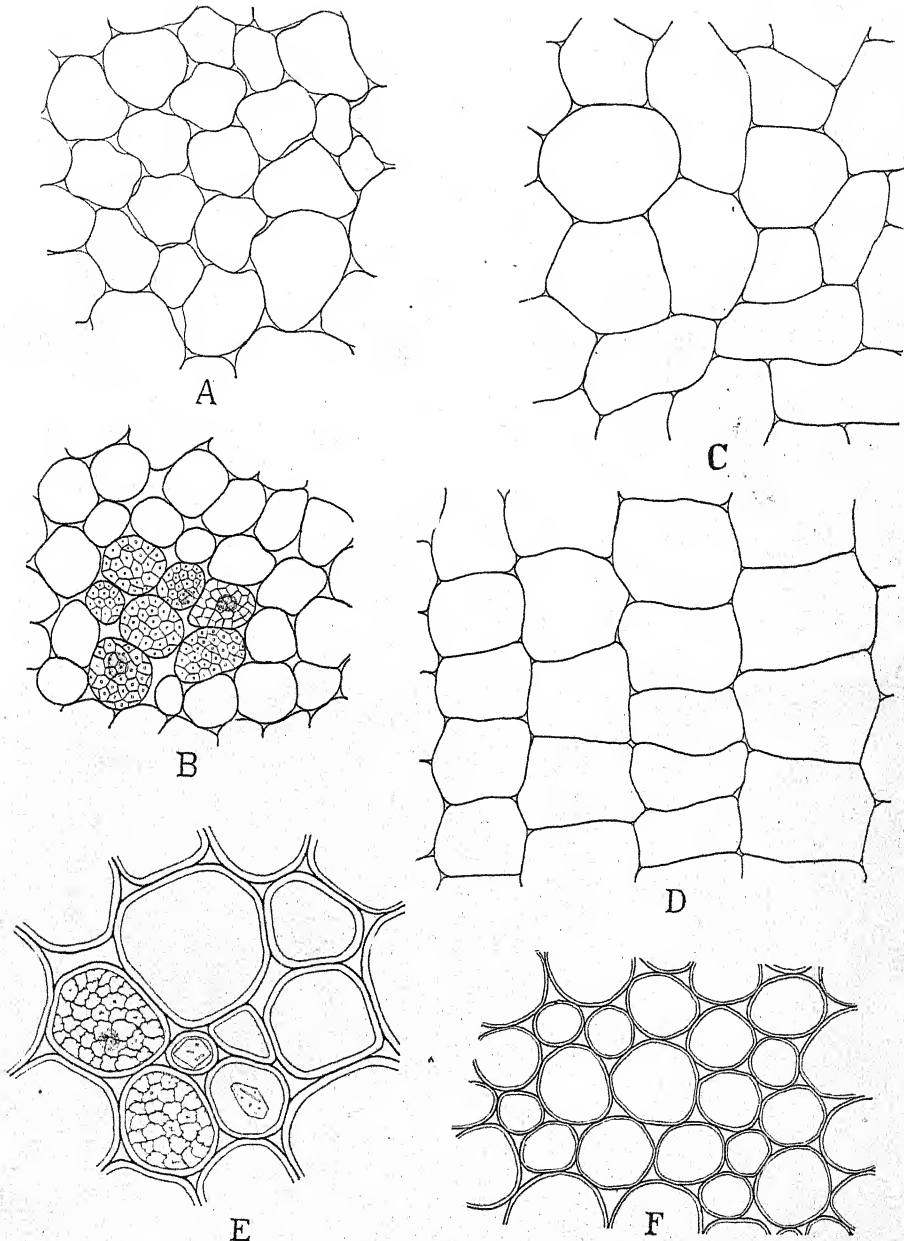


FIG. 30.—Parenchyma. *A*, from pith of rhizome of *Polypodium vulgare*. *B*, from cortex of root of *Asclepias incarnata*, the cells filled with starch grains. *C*, *D*, from pith of *Zea*, transverse and longitudinal respectively. *E*, thick-walled, lignified cells from pith of twig of *Castanea dentata*, the cells containing starch grains or crystals. *F*, thick-walled cells from pith of *Clematis virginiana*.

terms, however, are undesirable for the designation of tissue types. The other two common simple tissues, collenchyma and sclerenchyma, are supporting tissues. They are, however, different in specific function and in the cell types which make them up.

Collenchyma.—In the elongating parts of many stems, and less commonly in other parts, such as petioles and midribs of leaves, and in specialized stems, such as pedicels and peduncles, there occurs a type of supporting tissues adapted to changes incident to development. This is known as *collenchyma*. Such tissue is also sometimes found in mature plant parts which remain permanently soft. Collenchyma consists of elongate cells which remain alive after maturity, in contrast with the condition in sclerenchyma where the mature cell is usually without a living protoplast. The ends of the cells are at right angles to the sides, or oblique, or tapering, and the walls are markedly thickened. However, the walls are soft and plastic, being of cellulose containing a high percentage of water, and the thickening is irregular, the thicker areas being in the form of longitudinal strips. These thickened bands are chiefly in the corners of the cells, the sides remaining thin (Fig. 31, A, B, C). In some types of collenchyma cells the thickened areas cover the tangential walls rather than the corners (Fig. 31, E); in other cases the thickening is confined to those parts of the walls abutting on intercellular spaces (Fig. 31, D). The spaces are thus surrounded by thickened parts of walls, hollow-rod-like supporting structures are formed, and an appearance is given to the collenchyma which suggests thick-walled cells scattered among thin-walled cells. All three types are frequent, though thickening at the corners is the common condition. To a large extent the arrangement of the cells seems to control the type of collenchyma; where the cells are in definite tangential rows, lateral thickening is found, where the cells are irregularly arranged, corners are thickened, and where the cells are loosely arranged, the thickening is around the intercellular spaces. The types pass into one another and may even be found together in the same tissue. In cross section collenchyma cells are rounded or more or less angular. The walls are pitted with large simple pits, especially in a tangential direction. The cytoplasm is prominent, and may even contain chloroplasts, though photosynthesis is not commonly a function of this tissue. The contents of some cells of a strand of collenchyma may differ somewhat from those of others, for example, some being tannin-bearing and others not, as in *Rumex*; but collenchyma is always a simple tissue, and collenchyma cells are not found mingled with other cell types in a complex tissue. The limits of a band or area of collenchyma may be sharp, but more often the cells merge into the surrounding parenchyma or sclerenchyma by a series of transitional forms.

In the capability of collenchyma cells for elongation through the plasticity of their walls lies the adaptability of this tissue to growing

regions. Its thick walls, the interlocking of the cells to form long strands, and the position of these strands always at the periphery of the cortex, supply the strengthening qualities. Collenchyma necessarily develops early in the ontogeny of the region where it occurs.

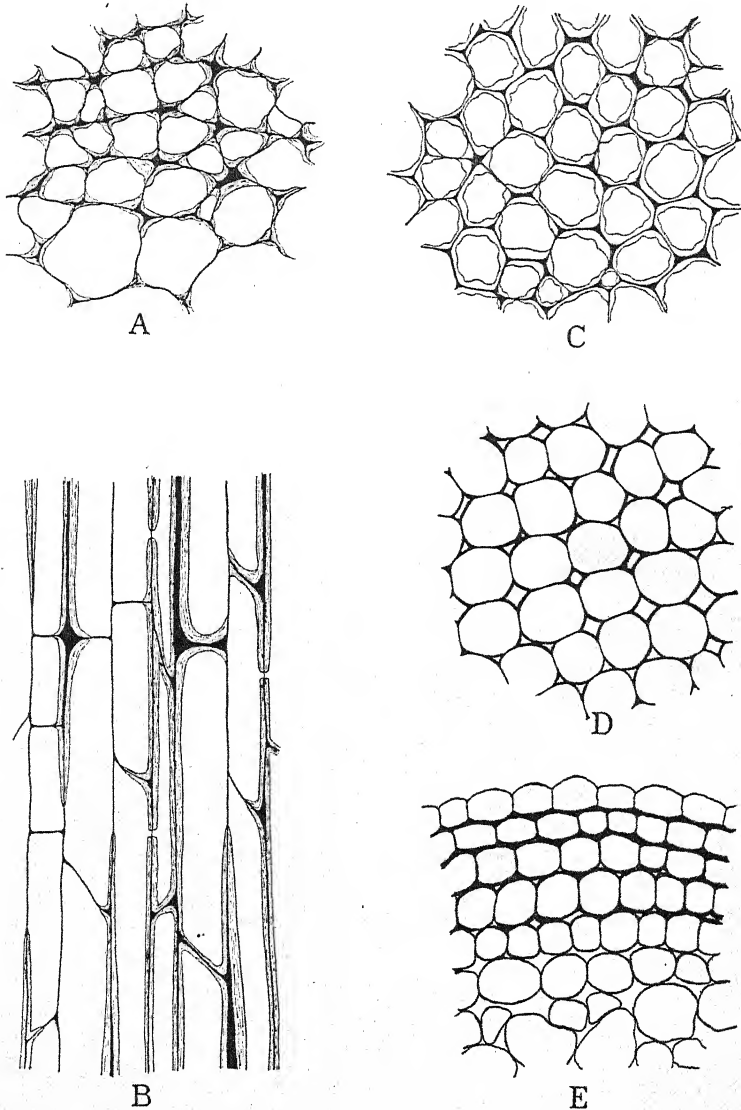


FIG. 31.—Collenchyma. A, B, transverse and longitudinal sections from stem of *Solanum tuberosum*. C, D, E, transverse sections from stem of *Abutilon Theophrasti*, stem of *Asclepias syriaca*, and petiole of *Asarum canadense*, respectively.

Two kinds of collenchyma may be distinguished, *temporary* and *permanent*. Temporary collenchyma is destroyed as secondary growth

in diameter takes place. It is crushed and flattened and may be removed by absorption. This condition obtains in many herbaceous plants which have considerable secondary thickening, such as *Melilotus*, *Chenopodium*, *Solidago*. The stems of typical woody plants rarely possess collenchyma, and roots are always without it, since support is unessential. Permanent collenchyma remains in a normal functional condition in mature plant parts. Petioles, such as those of *Solanum* and *Sambucus*, which are soft and not particularly woody, are supported largely by permanent collenchyma. Soft, herbaceous stems, such as those of *Impatiens* and *Pilea*, are also supported to a considerable extent in this way, and even the strongly woody stems of some herbs—for example, species of *Aster*, *Nepeta*, *Pelargonium*, *Rumex*, and *Lactuca*—possess small amounts of it.

Sclerenchyma.—In contrast with collenchyma, the other type of supporting and protecting tissue, *sclerenchyma*, has the walls of the cells definitely hard and lignified, with a low percentage of water; and the cells are in most cases without protoplasts, though sometimes scanty protoplasmic contents remain in the mature cell. The walls are much thickened, and uniformly so. In shape and size many kinds of cells occur in sclerenchyma, but two general types are recognized—*fibers* and *stone cells*.

Fibers.—Fibers are elongate sclerenchyma cells, usually with pointed ends (Figs. 34, 38). Chemically, the walls are usually lignified, although there are fibers with walls entirely of cellulose or with various percentages of cellulose, and others with mucilaginous walls. The pits of fibers are various in shape, but are always small, either round or slit-like in outline, and, in mature cells, unless a protoplast is present, are doubtless functionless. Pits may be numerous but are commonly rather few in number, and in fiber types with excessively thick walls they may be largely absent, or present only as vestigial structures. The lumen of fibers is small because of the space occupied by the thick wall; it often is a mere channel through the center of the fiber and this opening may be blocked in spots (Fig. 38, B), so that at certain levels in the fiber no lumen exists, only a line or spot representing, in cross section, its former position. In the development of fibers the protoplast often becomes multinucleate, the presence of additional nuclei being related possibly to the building up of a thick wall over so large an area. In most kinds of fibers, however, the protoplast disappears as the cell reaches maturity, and the permanent cell is dead and empty. Those kinds of fibers which retain their protoplasts, and other types of fibers, are discussed in more detail under the tissues in which they occur (see Xylem, Phloem, Cortex, etc.).

Classification of Fibers.—If the usual and loose use of the term “fiber”—such as is covered by the above definition—is accepted, fibers may occur in nearly all parts of the plant. They are most generally found and

are most abundant in the cortex, pericycle, phloem, and xylem. It is difficult to classify fibers either from a morphological or from a physiological viewpoint. However, morphologically, there are two distinct types. The fibers of the cortex, the pericycle, and the phloem possess simple pits and are thus different from those of the xylem, which have bordered pits (although these pits may be so reduced as to be essentially simple), since xylem fibers are, morphologically, reduced tracheids. Fibers are sometimes divided into two classes, bast fibers and wood fibers. These groups are essentially the same as the two just discussed, but the terms are poor, since the word "bast" is involved and this has, unfortunately, several uses. In its most common use, the term "bast" is synonymous with phloem, or refers to fibers of the secondary phloem. "Bast fibers" in the above classification include fibers of the cortex and pericycle as well as of the phloem. Fibers may best be designated by means of the tissue or region in which they occur, as cortical fibers, pericyclic fibers, phloem fibers, wood fibers, etc.

Fibers may occur singly or in small groups scattered among other cells. Usually they form strands or sheets of tissue extending longitudinally for considerable distances. Their value as strengthening tissue is largely due to their arrangement in these long masses and to the overlapping and interlocking of the cells. They serve also to give general firmness to tissues.

Stone Cells.—In contrast with fibers, stone cells are characterized by having diameters essentially alike, that is, the longer diameter of a stone cell may be much greater—even several times greater—than the shorter diameter, but not many times greater as it is in fibers (Fig. 32, *C, D, G, H*). Many cells will be found, of course, which are transitional in type between typical fibers and typical stone cells (Fig. 32, *A, B*). Such may be called short, stone-cell-like fibers, or elongate stone cells. Stone cells may be roughly rounded, polyhedral, short-cylindrical, or very irregular (Fig. 32), but, in general, are without definite form. When in masses they often vary greatly in size and shape, resembling nothing so much as a heap of stones. They may lie loosely together, or, when angular, may be closely packed.

Several other terms are applied to stone cells. The term *scleireid*, meaning a hard, protecting cell, in contrast with *tracheid*, a conducting cell, is often used as synonymous with stone cell; but, unfortunately, this term may indicate any sclerenchymatous cell. In occasional use it is restricted to the special type of sclerenchyma which, as columnar or branched cells, reinforces photosynthetic tissue in xerophytic leaves. The term *stereid* is obsolete. Stone cells are also known as *sclerotic cells*, and, when in leaves and fleshy fruits, as *grit cells*. The gritty parts of the flesh of pears and quinces are clusters of stone cells (Fig. 32, *D*).

Stone cells occur almost anywhere in the plant body, but they are most abundant in the cortex, in the phloem, and in fruits and seeds.

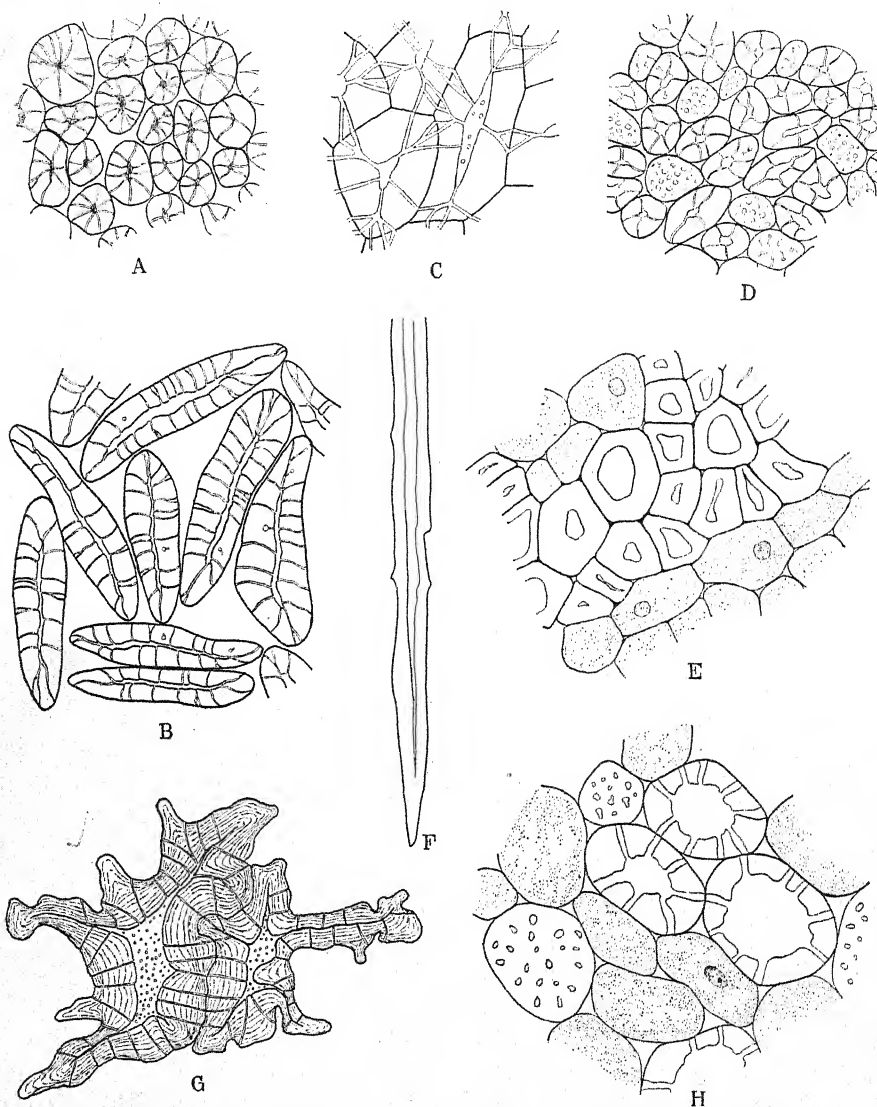


FIG. 32.—Sclerenchyma. A, B, transverse and longitudinal sections of elongate stone cells from endocarp of *Cocos nucifera* (coconut shell). C, stone cells from endocarp of *Crataegus*; the pits are fused in groups. D, stone cells ("grit cells"), from the fleshy pericarp of *Pyrus communis*. E, fibers in transverse section in the pericycle of *Cannabis*. F, longitudinal section of part of one fiber shown in E. G, irregular stone cells from the phloem of *Tsuga*. H, stone cells from the stem cortex of *Dracaena fragrans*.

Like fibers, they occur singly, in groups of a few cells, or in very large masses. The hard parts of seeds, nuts, and hard fruits generally are

made up largely of stone cells of various types. Where stone cells are scattered, they merely give firmness, as in leaves, flesh of fruits, etc. In masses, they give hardness and mechanical protection, as in many kinds of bark, in the shells of nuts, etc.

The wall of stone cells is very thick and strongly lignified. Occasionally, it is suberized or cutinized. The pits are very small, are always round in outline, and are found to form more or less branching canals because of the fact that, as the area of the cell wall is reduced on the inside by the increased thickening, the pits are brought together (Fig. 32, A, C). Two or even several pits thus fuse to form one structure, which has but one mouth in each cell, but has as many arms as there were original pits. Stone cells are dead cells. Sometimes the shriveled remains of protoplasm, and in other cases the contents of the protoplast, such as tannin and mucilage, are present.

THE IMPORTANT COMPLEX TISSUES

The structural and functional prominence of the vascular system renders its tissues of great importance as tissue types. These vascular tissues are, in fact, the only complex tissues which need separate discussion; all others may be interpreted as combinations of parenchyma and sclerenchyma, and of modifications of these tissues. The following treatment of vascular tissues is of general nature only, since a description of xylem and phloem as primary and as secondary tissues, and as specially modified in various organs, will be found in other chapters.

XYLEM

The Tracheid.—The fundamental cell type in xylem is the *tracheid*. The tracheid is an elongate cell with tapering ends (Fig. 33), which, when mature, is non-living, that is, without a protoplast. The walls are thick and in most cases lignified. In cross section the tracheid is typically angular, though more or less rounded forms also occur. The tracheids of secondary xylem, owing to their method of arrangement, have fewer sides than do those of primary xylem, and are more sharply angular, often definitely rectangular in cross section. The ends of the tracheids do not taper uniformly to the tip in all planes, but the tapering is confined, in secondary xylem, largely to the radial plane, and is often on one side of the cell only. The end of a tracheid may thus be more or less chisel-like. The tapering is seen in tangential sections of the tracheid; radial sections do not show tapering, the end of the cell in such sections being rectangular or somewhat rounded. The pits are abundant and are always of the bordered type, though they vary in size, in outline, and in distribution over the walls. The lumen of a tracheid is large and free of contents of any kind. The tracheid is thus apparently well adapted structurally to its functions, which are, primarily, water conduction, secondarily,

support. It is a long, empty, firm-walled tube extending parallel with the long axis of the organ. It is in communication with contiguous

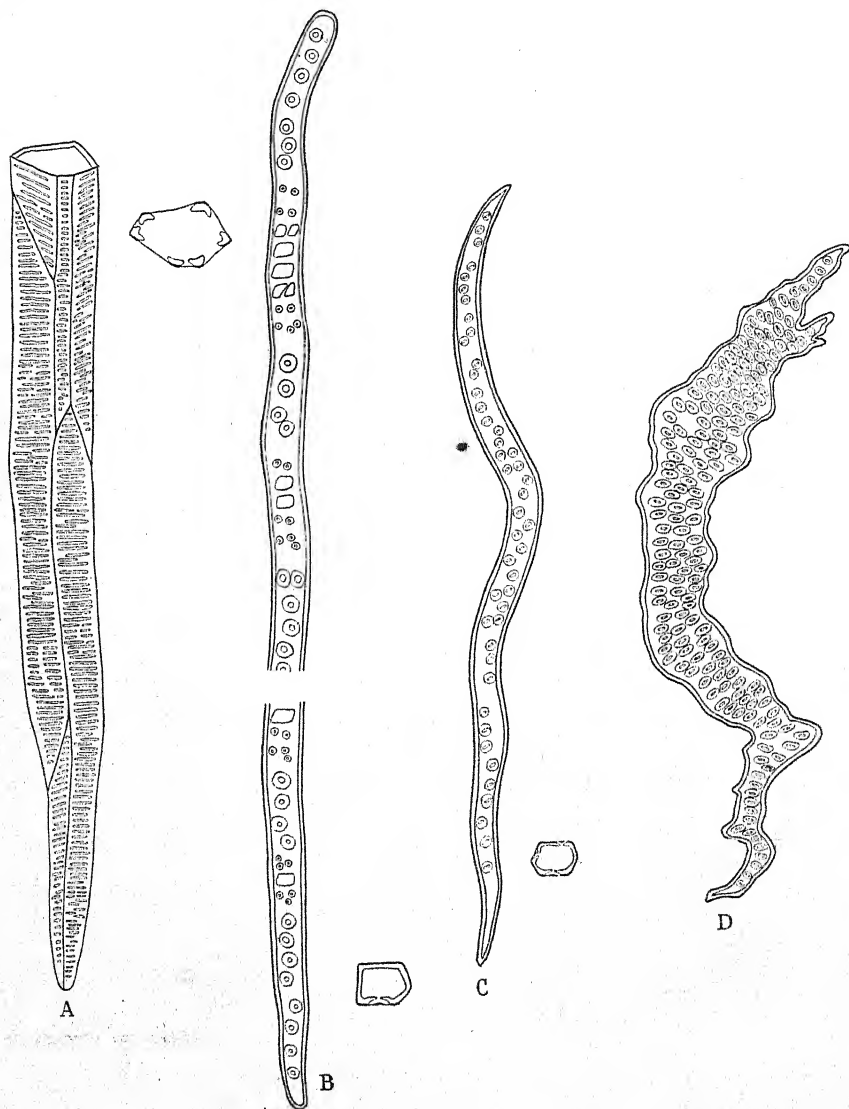


FIG. 33.—Tracheids. A, from *Woodwardia virginica*, one-sixth of cell shown. B, from *Pinus Strobus*, one-third of cell shown. C, D, from *Quercus alba*, C, a normal, and D, a flattened and distorted tracheid from the spring wood. (The illustrations of tracheids are drawn to scale and to the same scale as are those of fibers and vessels.)

tracheids—as well as with other types of cells, living and nonliving—by means of pits. These thin areas permit ready diffusion into adjacent cells. The arrangement of tracheids is always such that contiguous

cells overlap, at least over the tapering portions, and over these areas of the wall the pits are often abundant. Channels for longitudinal conduction are thus provided through a series of lumina which form a more or less direct line, or an anastomosing system.

The Continuity of the Walls of the Tracheid.—The individual lumina are shut off from one another by thick walls, and, in the pits, by the closing membranes. The closing membranes, however, except in the central region, the torus, are very delicate, and at least in some cases are perforated. In many gymnosperms, for example, *Larix* and *Sequoia*, the perforations, though microscopically minute, are so numerous that the torus is suspended by a meshwork of strands (Fig. 16, A). In such cases the openings are not readily seen unless the membrane is well stained, but their presence is demonstrable, since solid particles such as those of carbon in India ink pass under pressure from one tracheid to another through the pits. This condition is an approach to that found in vessels where large openings occur between water-conducting cells.

Bordered Pits.—The position of pits in the wall of the tracheid and the size and shape of pits depend upon the position and nature of the contiguous cells. The various larger plant groups are characterized by more or less constant types of bordered pits which have definite shape, extent of border, etc. Thus the ferns and the clubmosses have transversely elongated pits with narrow borders and little or no torus. The pits lie close together, covering the wall, giving it a ladder-like appearance (Fig. 33, A), whence the name *scalariform tracheid*, or, better, *scalariform pitted tracheid*, is derived. The former term is undesirable in this connection, since it is also used with other meanings, and where definite pits do not occur (Chap. V). In the gymnosperms and angiosperms the bordered pits are chiefly rounded with wide borders (Fig. 33, B, C), those of the angiosperms being mostly much smaller. The best development of the torus is in the gymnosperms, where the bordered pit in tracheids probably reaches its highest development (Figs. 16, 17). The closing membrane of such pits is so constructed that its position in the pit cavity may be readily changed from a median position to a lateral one with the torus closely appressed to the aperture of the pit (Figs. 15, C; 16, B, C). A return to the median position and a movement to the opposite side of the pit cavity are accomplished with equal readiness. A valve-like action is thus secured, the pit being freely open when the torus is in the median position, diffusion—or, in perforated closing membranes, direct passage—taking place around the torus through the peripheral part of the closing membrane. When one of the pit mouths is closed by the placing of the torus against it, direct passage is largely or wholly shut off, and diffusion must take place through the thicker and denser torus. Thus, apparently by changes in the position of the closing membranes of bordered pits, some control over the passage of fluids in xylem may be had. It is

significant that the type of pit in which this control of the passage of fluids is present is characteristic of water-conducting cells and does not occur elsewhere; also that in the somewhat reduced pits of fiber tracheids and fibers the pit membranes have lost the capability for movement. The bordered pit will be found further discussed in Chaps. II and VII. In simple pits no structural complexity occurs.

Function of the Tracheid.—Thus the tracheid is structurally adapted, both in lumen and in wall, to the function of conduction. The thick and firm walls of tracheids also aid in support, and, where there are no fibers or other supporting cells, the tracheids play a prominent part in the support of an organ. For this the overlapping and interlocking of the cells, and their union into strands and cylinders, are, of course, as important as are thick walls.

Tracheids alone probably made up the xylem of very ancient plants, but in living forms wood is a complex tissue, there being present even in the simplest forms of secondary xylem parenchymatous wood rays; and primary xylem (as a morphological tissue unit) always contains parenchyma cells. The more complex types of xylem may contain several kinds of cells—tracheids; fibers of one or more kinds; vessels of one or even of two types; parenchyma cells, known as *xylem parenchyma*, or *wood parenchyma*; and *wood-ray parenchyma*. Further discussion of the constitution of xylem will be found in Chap. VII.

The tracheid clearly serves both as a conducting and as a supporting cell. However, evolutionary development in xylem has resulted in a specialization of this once simple tissue in such a way that the original functions of the tissue have become segregated, and relegated to distinct cell types—support to fibers of various kinds, and conduction (of an apparently more efficient type) to vessels. The new function of food storage has been acquired, and this is carried on by wood parenchyma. The wood-ray parenchyma is also concerned with food storage; the ray is, however, probably primarily concerned with lateral food conduction. In most complex xylem in which the definitely dissociated functions of support and conduction are given over to fibers and vessels respectively, tracheids are not found. In the wood of *Quercus*, and of some other genera, however, all three kinds of cells are present (Fig. 82).

Wood Fibers.—In the phylogenetic development of the fiber, the thickness of the wall has been increased and the diameter of the lumen correspondingly decreased; the length of the cell, especially of the tapering end, in many cases increased, and the number and size of the pits reduced. This reduction of the pit in size is discussed in detail in Chap. II. Where reduction has reached a stage where the lumen is so narrow and the pits so small that it is apparent that there can be but little if any conduction, typical fibers are formed. Between such cells and normal tracheids all intergrading forms occur. These intermediate types,

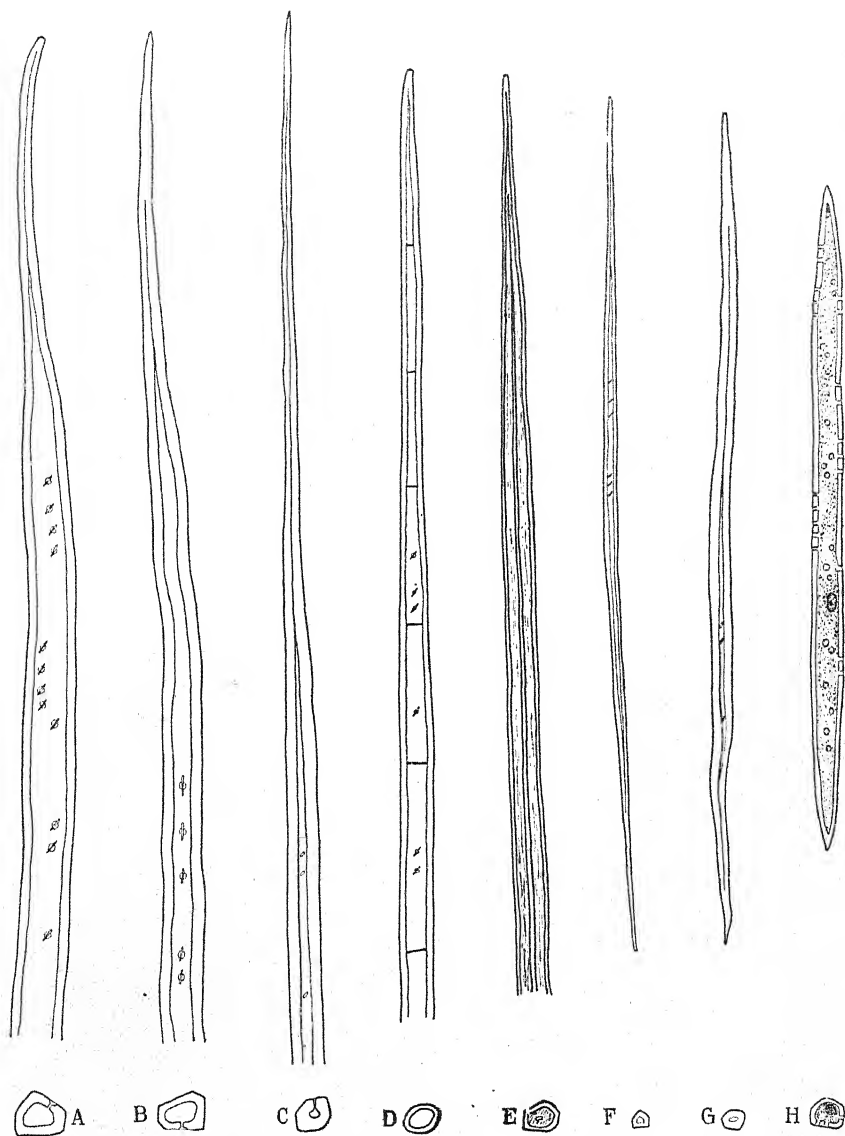


FIG. 34.—Wood fibers. A, typical fiber, from *Pyrus Malus*, two-thirds shown. B, typical fiber, from *Liriodendron Tulipifera*, two-thirds shown. C, libriform fiber, from *Quercus alba*, one-fourth shown. D, septate fiber, from *Swietenia Mahagani*, one-half shown. E, mucilaginous fiber, from *Quercus rubra*. F, libriform fiber, from *Carya ovata*. G, libriform fiber, from *Guaiacum sanctum* (lignum vitae). H, substitute fiber, from first annual ring of *Sassafras variifolium*.

which cannot be called either typical tracheids or typical fibers, are designated *fiber tracheids*. A line between tracheids and fiber tracheids or between fiber tracheids and fibers cannot, of course, be drawn. More extreme fiber development results in the formation of a type of fiber with very thick walls and with pits so reduced as to be essentially simple (Fig. 34, *C, F, G*). Such fibers are called *libriform fibers*, because of their similarity to phloem fibers (phloem or phloem fibers having been known to early students as *liber*). Libriform fibers occur abundantly in woody dicotyledons, chiefly in the more specialized families, such as the Leguminosae. Another type of fibers has partitions, or *septa*, dividing the lumen transversely into compartments. The dividing plates in these *septate fibers* are always thin and cellulose in nature, in strong contrast with the heavy, lignified, lateral walls (Fig. 34, *D*). The function of the septa is unknown. Septate fibers occur in many plants, but especially in shrubs, the more "woody" herbs, in vines, and in tropical trees. A septate fiber may readily be distinguished from a row of parenchyma cells by the lack on the septa of secondary walls corresponding to those on the lateral walls, and by the fact that the middle-lamella-like septum does not extend to the middle lamella of the side walls but ends at the surface of the secondary wall. A peculiar type of fiber is that known as the *substitute fiber* (Fig. 34, *H*). This differs markedly from all other fibers in that it is a living cell. Its pits are simple. The thick wall serves as a mechanical supporting feature, and the protoplast as a food-storage region. This cell is thus functionally and structurally a combination of fiber and parenchyma cell. It occurs commonly in dicotyledonous herbs, and often in shrubs and woody vines.

Vessels.—Specialization of the tracheid in the direction of adaptation to water conduction has resulted in the enlargement of the cell, the lumen becoming wide, and in the perforation of the wall by large openings so that transmission may take place directly from cell to cell (Fig. 35). The wall thickness remains about as in the tracheid, or is thinner, though vessels with very thick walls are frequently found, as in *Carya*, *Fraxinus*, and *Diospyros*. The pits are often more numerous and smaller than are those of tracheids and may cover the wall closely. When abundant, they may be scattered or arranged according to some definite geometrical plan. The distribution of pits is, of course, controlled primarily by the nature and the position of the contiguous cells. Thus, if another vessel is contiguous to the vessel in question, the wall is heavily pitted over that part of its surface between the two vessels, whereas only a few small pits or none exist in the area lying against a fiber. The pits between a vessel and tracheids, wood parenchyma cells, and wood-ray cells are likewise, in large measure, controlled in position, number, and type by the pitting normal to these cells.



FIG. 35.—Vessels in side view and cross section. A, B, from *Betula alba*. C, D, from *Liriodendron*. E, F, from *Lobelia cardinalis*. G, H, from *Quercus alba*. I, J, from *Pyrus Malus*. K, from *Acer Negundo*. L, M, from *Quercus alba*. N, end of vessel from *Lobelia* showing perforation indicating derivation of porous vessel from scalariform. O, ends of vessels from *Lobelia*, showing method of union of vessel units in a series.

With increase in size of the vessel goes a reduction (phylogenetically) in length. This shortening becomes excessive as the diameter becomes correspondingly great, so that in the larger type of vessels the cell is broader than it is high. Accompanying the shortening, and doubtless due in part to this modification, the ends of the cell change in shape, the angle made by the tapering end wall with the side wall becoming greater and greater until the end wall is at right angles with the side wall. Thus the larger vessel cells are cylindrical, the most extreme forms being drum-shaped.

Uses of the Term "Vessel."—Since the perforations of the cell occur usually in the end walls, the development of end walls transverse to the long axis of the cell brings a series of cells into a definite tube-like system, which provides for transmission in a more or less nearly straight line. Such a condition is in contrast with the indirect lines of conduction in a group of tracheids. A tube-like series of cells thus formed has long been known as a *vessel*, or *trachea*. However, these terms, like so many others, have, unfortunately, two meanings. They were first applied to the definite, open tubes of wood, that is, to what are now recognized as series of cells united into a system, much as pieces of water pipe are placed together to form a pipe line. The terms are also used to indicate the individual cells which make up such series. When the end walls of these cells are markedly oblique, definite direct tubes, or lines of conduction, are not set off; and, further, in these cases the individual cell stands out, whereas in the tube-like series the individual cell is not evident to superficial examination. The use of the terms "vessel" and "trachea" as indicating series of cells has the support of priority, as well as that of long-continued usage. A restriction of the terms to this meaning, however, seems hardly practicable, since there exists for the units of the vessel no term other than *vessel segment*, or *vessel unit*, and these are not satisfactory in that they do not suggest homology with tracheid and fiber. Further, where definite direct series of open water-conducting cells do not exist, these latter terms are wholly inappropriate. It seems better, therefore, to continue the double usage of the terms, since the context will in most cases make clear the sense in which the word is used; and to use *vessel element* for the individual cell whenever necessary to avoid ambiguity. The terms *vessel segment* and *vessel unit* may also be used in this sense, but are less desirable.

Types of Perforations in Vessels.—The perforations of a vessel are confined to the end walls except in certain slender tapering types, where definite end walls do not exist; in such cells the perforations occur on the side walls. Two perforations occur in most vessels, one in either end, but three and even four are sometimes found, each opening into a different cell. Two types of perforations occur: one where the opening is single and commonly large and more or less rounded, a *simple perforation*

(Fig. 35, *G, I, K, L*); the other where two to several smaller openings are clustered, forming an aperture divided by transverse bars, a *scalariform perforation* (Fig. 35, *A, C, O*). Simple perforations vary in shape from round to narrowly elliptical. They occur both on end walls which are transverse to the long axis of the cell and on those which are oblique, but scalariform perforations are found only on the inclined walls, and chiefly on the more strongly oblique ones. Vessels with simple perforations are known as *porous vessels* and those with scalariform openings as *scalariform vessels*. In the latter type the pitting of the side walls may also be scalariform or the pits may be circular and arranged in any one of several ways. That the perforations of vessels represent enlarged and fused bordered pits from which the closing membranes have disappeared is clear. All transitional stages are frequently found; occasionally, a single end wall shows typical, normal bordered pits, similar pits without membranes, and semifused groups of two or more pits. This fusion is, of course, not ontogenetic but phylogenetic.

In porous vessels the proportion of the end wall occupied by the perforation is greatest where the wall is transverse; under this condition the wall is reduced to a narrow rim, and in extreme cases may be almost or quite lacking. The limit of the vessel units is always made clear, however, by the segmentation of the lateral wall, and frequently also by the median bulging of the walls of the individual cells. A given species or genus may possess one type of vessel exclusively, or both types may be present in the same tissue. In the latter case the larger vessels are more commonly porous and the smaller ones scalariform.

The vessels of the secondary wood in many plants possess tertiary thickenings (Fig. 14). The functional significance of these is unknown.

Though vessels characteristically are wide, the more slender forms are even narrower than are typical tracheids. From this diameter there is a range to a maximum of somewhat over one millimeter. The wider vessels are characteristic of certain herbs, such as *Zea*, many woody vines and lianas, and of some trees, as, for example, *Castanea*, *Quercus*, and *Fraxinus*.

Vessels are characteristic of the angiosperms; only in a few forms are they lacking—certain genera of the Magnoliaceae, the Trochodendraceae, some of the Cactaceae, and many parasitic and aquatic groups. In some of these their absence is doubtless due to loss through phylogenetic reduction and specialization. Vessels also occur in the Gnetales, though not elsewhere in the gymnosperms, and to some extent in the ferns. The frequency of occurrence of vessels in the ferns is in question; in this group the perforations are merely exaggerated pits without membranes.

Wood Parenchyma.—In the majority of cases parenchyma cells, other than those of the wood rays, occur as constituents of xylem. In

this tissue they form vertical series of more or less elongate cells placed end to end (Figs. 36, 82). In amount, parenchyma in wood, in addition to that in the rays, varies from none, as in the wood of certain conifers, such as *Pinus*, *Araucaria*, and *Taxus*, to a considerable proportion, as in many dicotyledons. In primary wood, except in more specialized types, there is always a considerable amount, especially in the first-formed portions. The xylem parenchyma cells may be thin-walled or thick-walled, those of secondary wood often having thick, more or less strongly lignified walls. In function, wood parenchyma serves for food storage and is probably also associated with conduction, either directly or indirectly. Those parenchyma cells which constitute the xylem rays are considered in the discussion of secondary xylem.

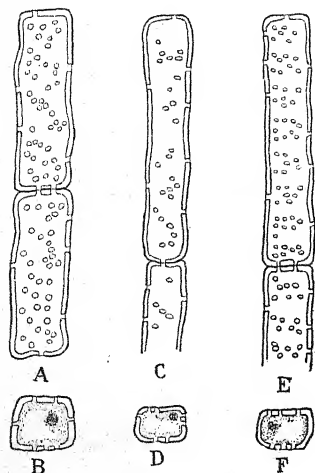


FIG. 36.—Wood parenchyma cells in longitudinal and transverse section (the protoplasts omitted in the longitudinal). A, B, from *Quercus alba*; C, D, from *Pyrus Malus*; E, F, from *Carya ovata*. (The scale of this figure is twice that of the figures of tracheids, fibers, and vessels.)

Function of Xylem.—That the xylem as a whole is the water-conducting tissue and the chief supporting structure of vascular plants is without question. The secondary functions of food storage—such as the storage of starch in wood parenchyma and xylem rays, especially in roots of woody plants—and of secretion—as of resin in the pine—are also obvious. It has been established beyond doubt that water conduction takes place in the lumina of tracheids and vessels. The problem of the rise of sap through these cells, however, is still unsolved. Whether physical processes directly and alone are concerned, or whether the activities of living cells

are also involved, has long been in dispute. Histological evidence strongly suggests that the presence of living cells is necessary to the upward conduction of water by tracheids and vessels. Every water-conducting cell is in contact in some part of its wall surface with one or more living cells, and abundant pits are present in this contact area. In highly specialized wood, where the tissue consists largely of fibers, and where the water-conducting cells—in such cases porous vessels—are relatively few, each vessel is ensheathed with parenchyma cells and no parenchyma cells occur among the non-conducting fibers. Thus, there seems to be a definite correlation between the presence of parenchyma and water conduction.

PHLOEM

Sieve Tubes.—Just as in the xylem the tracheid is the fundamental structural and functional cell type, so in the phloem the *sieve tube* is the important cell type. The phloem is, like the xylem, a complex tissue. It may contain only sieve tubes and *phloem parenchyma*, as in the pteridophytes and many gymnosperms, or it may consist of several cell types—sieve tubes, *companion cells*, phloem parenchyma of one or more kinds, *phloem fibers*, stone cells, and various kinds of secretory cells.

As in the xylem the tracheid has undergone evolutionary specialization, so the sieve tube likewise has been considerably modified in the course of its phylogenetic development. The specialization, however, is parallel only in that cell types which are probably more efficient as conducting structures have been developed. The sieve tube has been broadened and shortened, the end wall becoming less and less oblique and ultimately transverse, but apparently in no case is the cell wider than high, as is the most specialized type of vessel. Probably no new cell types have been developed in evolution from the primitive sieve tube, since the sieve tube has not, like the tracheid, a double function. It is a conducting cell only. The simple phloem parenchyma of the more primitive plants has doubtless given rise in complex phloem to two or more kinds of parenchyma, and also to the fibers and the stone cells of this tissue.

Uses of the Term "Sieve Tube."—In the use of the term "sieve tube" the same difficulty exists as with the term "vessel." The term "sieve tube" is given to a series of cells; it is also applied to the individual cell in such series, and is even more frequently so used. To the individual cell, *sieve-tube element*, *sieve-tube segment*, and *sieve-tube unit* are also applied. Since in the lower, and in some higher, forms no definite linear series of cells can be distinguished, it appears necessary—unless new terms are coined—to continue the loose double use of the term. This is possible without resulting uncertainty, since the context will in most cases indicate the exact meaning. The terms "sieve-tube element" and "sieve-tube unit" are, however, free of ambiguous meaning.

Structure of the Sieve Tube.—The sieve tube is an elongate living cell with a thin cellulose wall (Fig. 37). The protoplast of this cell has a large central vacuole and the cytoplasm forms a thin peripheral layer, in which, according to the widely accepted opinion, no nucleus is present when the cell is mature. These cells are arranged more or less definitely in longitudinal rows and form a series by the connection of their protoplasts through small openings in the wall. These perforations occur in groups in restricted thin areas which are known as *sieve plates*. The limits of the sieve plates are not as well defined in pteridophytes and in gymnosperms as in the angiosperms where they are sharply set off from

the thicker part of the wall. The sieve plate is divided into *sieve fields* by a network of thicker strips. The sieve fields, like the sieve plates, are not sharply defined in lower forms, but become so in the angiosperms, the bars between becoming more clean-cut and increasingly thick. Through each sieve field in the pteridophytes and the gymnosperms pass several to many plasmodesma-like strands. In these cases the sieve field is hardly to be distinguished in general structure and appearance from a simple pit with its plasmodesma; the protoplasmic strands are, however, of larger diameter. In angiosperms the sieve field as such is not present, the entire area being occupied by one large protoplasmic strand. This strand appears to represent the fused and enlarged group of connecting threads of the lower plants, the area of wall occupied by the sieve field having been lost.

The perforation of the wall by conspicuous cytoplasmic strands and the absence of a nucleus are the outstanding structural features of the sieve tube. Some question has arisen as to the absence of the nucleus; it has been suggested that nuclear substance is possibly present in a diffused or scattered state; also, that when the nucleus has disappeared, the sieve tube is already degenerate, and that its life as a functioning conducting cell is over at this stage. On histological evidence the latter condition seems unlikely, since the nucleus apparently disappears with, or just before, the attainment of full size in the cell, and the sieve tube may remain for sometime, even for several years, without further structural change.

In shape, sieve tubes cover a range similar to that of the tracheid-vessel series: in pteridophytes and gymnosperms the ends of the cells are long-tapering, and an end wall as distinct from a side wall is not apparent (Fig. 37, A, C); in angiosperms a similar type is also present, but in the majority of cases there is a well-defined end wall which is oblique (Figs. 37, E, H, M; 90, B, D), or, in the most specialized forms, transverse (Figs. 37, P, S; 91, C). The sieve plates are scattered over the side and end walls, or are restricted to certain walls, as to the radial and end walls in the sieve tubes with long-tapering ends; but they are more or less restricted to the end walls where the cell tapers more abruptly or has a transverse end wall. The number of plates on the side walls varies greatly: there are usually few or none where the end wall is transverse or nearly so (Fig. 37, P, S); where the end wall is long-tapering, the side wall—as well as the end wall from which it is hardly to be distinguished—may be completely covered by closely set sieve plates (Figs. 37, E; 90, B). The presence, number, and position of sieve plates is to a large extent controlled by the position and the arrangement of the surrounding sieve tubes. Sieve-tube elements may be somewhat lobed or forked and may even have three definite projections connecting with the ends of as many other sieve-tube elements. Where well-marked sieve

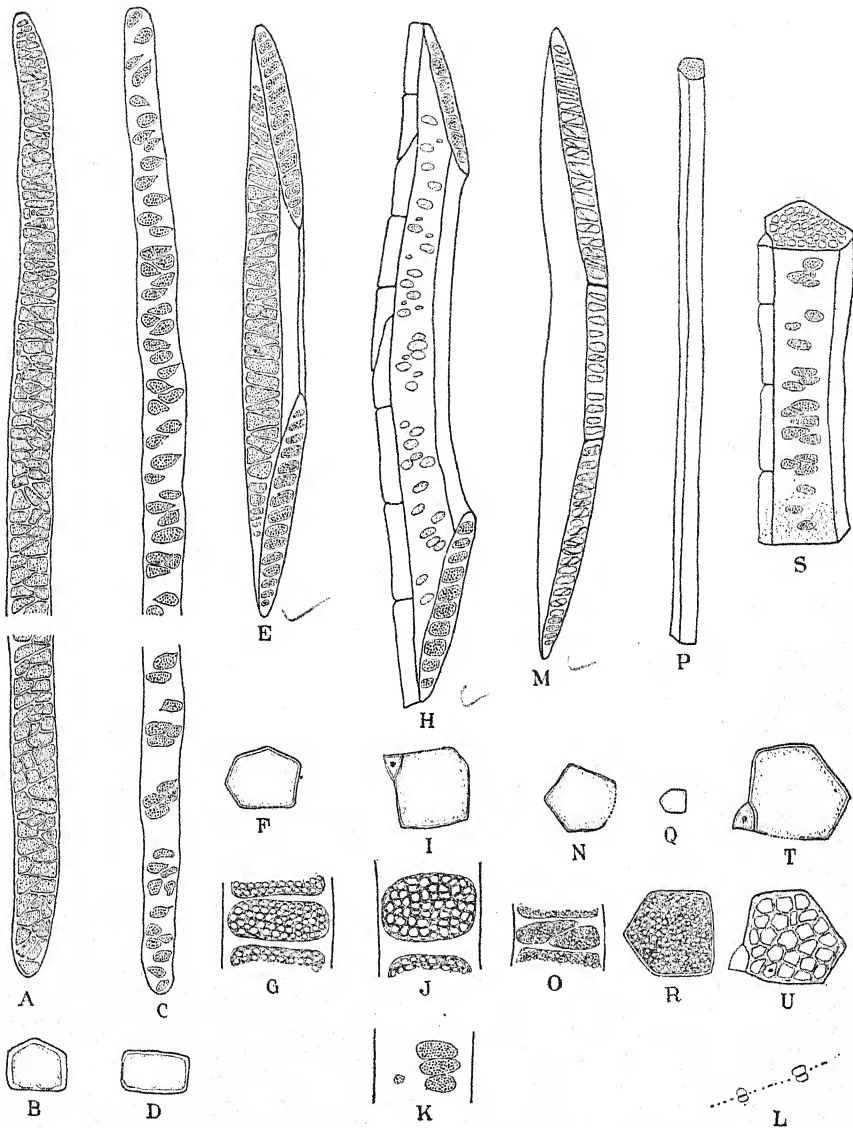


FIG. 37.—Sieve tubes in side view and cross section, with detail structure of sieve plates in some cases. A, B, from *Pteris aquilina*, only one-fourth of cell shown. C, D, from *Tsuga canadensis*, only one-third of cell shown. E, F, G, from *Juglans nigra*; G, part of sieve plate in detail. H, I, J, K, L, from *Liriodendron*; H, I, with companion cells attached; J, K, detail of sieve plate and of lattice respectively; L, sieve plate in section. M, N, O, from *Pyrus Malus*; O, detail of sieve plate. P, Q, R, from *Solanum tuberosum*; R, detail of sieve plate. S, T, U, from *Robinia Pseudo-Acacia*, with companion cells attached; U, detail of sieve plate. (The sieve tubes are drawn on the same scale as tracheids, vessels, and fibers. All enlargements of sieve plates and lattices are on the same scale.)

plates are lacking on the side walls, vestigial plates, known as *lattices*, are often present (Figs. 37, *H*, *S*; 91, *A*). These resemble typical plates of various types, but are indefinite and often ghost-like; the perforations are exceedingly minute, being often no larger than normal plasmodesma (Fig. 37, *K*), and in some cases are perhaps lacking. Stages intermediate between typical sieve plates and lattices may be found; such plates show few perforations and these are much smaller than are those of the normal plates.

As in the vessel, the more nearly transverse the end wall the fewer the perforations, until in the end wall which is transverse, the perforation is solitary; so in the sieve tube, the number of plates becomes less and less, and these become correspondingly more sharply defined and their pores larger the more nearly transverse the end wall, until but a single plate occurs in the wall which is at right angles to the side walls. In the latter type the largest pores occur (Fig. 37, *S*, *U*).

Contents of Sieve Tubes.—The cytoplasm of sieve tubes forms a thin layer about a large central vacuole; it may contain a few leucoplasts and scattered starch grains, but is not densely granular. The cell sap contains in solution protein compounds which are often of slimy nature. In some plants this albuminoid substance is abundant, and after the cells have been killed and fixed is found in a coagulated mass usually consisting of two prominent portions which lie against the sieve plates at the ends of the cell, and which are connected by a slender median portion. In other cases, the parts of the coagulated material are entirely separate, or may be drawn together into a single mass. Since projections of these masses penetrate and fill the pores of the sieve plates; the protein masses are known as *slime plugs* (Figs. 90, *C*; 91, *C*). The plug at the lower end is usually larger than that at the upper end of a cell. Whether the protein substances are aggregated in this way at the ends of the cell in the normal living sieve tube, or are uniformly distributed through the vacuole, or are collected chiefly in the center, seems to be in question. Cell sap with abundant slimy proteins is characteristic of many sieve tubes with transverse end walls.

Callus.—As sieve tubes cease to function, either temporarily or permanently, the sieve plates may be covered by a closing substance in cap-like masses, which are known as *callus*, or *callus pads*. These masses consist of the carbohydrate, *callose*, which is a colorless, glistening, highly refractive substance. The callus pads cover the sieve plates completely, often becoming quite thick, and projections penetrate the pores. Thus, when callus is present, communication between the cells appears to be cut down or entirely prevented. Callus does not form over typical lattices, a fact which in itself is evidence of their lack of function as sieve plates. The callus which forms at the approach of a rest period, *seasonal callus*, may be dissolved as activity again comes on, as in the spring in

some woody plants, but most callus is *definitive*, limiting finally the activity of the cell. Such callus is said to form in all old sieve tubes, but this is questionable, since in some species no callus deposits have been seen.

Phloem Parenchyma.—Several types of parenchyma cells may occur in the phloem (Fig. 39). These have been distinguished as *cambiform parenchyma*, *divided cambiform parenchyma*, and *conducting parenchyma*. The various types, however, are not sufficiently different to render this distinction of value. Cambiform cells are elongate tapering cells, in size and shape suggestive of cambium cells, as the term implies; divided cambiform cells result from the transverse division of cambiform cells; conducting parenchyma cells are shorter, broader cells with transverse end walls.

Companion Cells.—The *companion cell* is a special type of parenchyma cell associated structurally and functionally with the sieve tube. In the development of the sieve tube from the sieve-tube mother cell, a longitudinal division occurring soon after its formation by the cambium cuts off the companion-cell mother cell. Such is the plane of this division that the companion cell, when seen in transverse section, is usually a small triangular, rounded, or rectangular cell at a corner or along one side of the sieve tube (Fig. 37, *I*, *T*). The position of companion cells, especially in primary phloem, is sometimes such that it cannot be readily determined with which particular sieve tubes they are associated. This is frequently the condition where more than one longitudinal division has occurred, and where, therefore, two or more companion cells accompanying a single sieve tube appear in cross section. When seen in longitudinal section, the companion cell is an elongate, usually slender

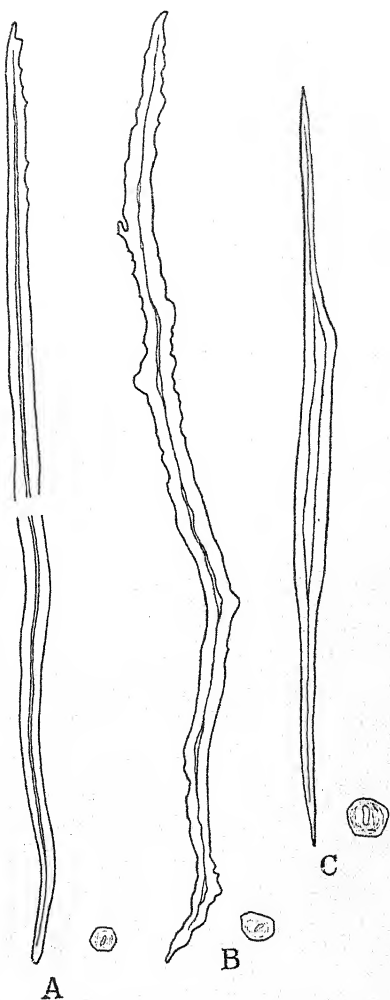


FIG. 38—Phloem fibers, longitudinal and transverse sections. *A*, from *Salix nigra*, only two-thirds of cell shown. *B*, from *Pyrus Malus*. *C*, from *Robinia Pseudo-Acacia*. (The scale is twice that of the figure of sieve tubes.)

cell of somewhat unsymmetrical shape. It may extend only one-half or one-third the length of the sieve-tube element, or quite its full length; or, because of transverse division in the companion-cell mother cell, there may be a row of several short, cylindrical cells extending the length (Fig. 37, *H*, *S*) or part of the length of a sieve-tube element. Thus, a sieve-tube element may be accompanied by one to several companion cells. In a given species there is considerable constancy, however, in the number of companion cells accompanying such a cell. The solitary, very long companion cells seem to be more frequently found in primary phloem and in herbaceous plants; the short and numerous companion cells appear to be characteristic of the secondary phloem of woody plants. In some plants companion cells are present with every sieve tube; in others, as in *Solanum tuberosum*, part of the sieve tubes are without them. However, companion cells doubtless occur in all angio-

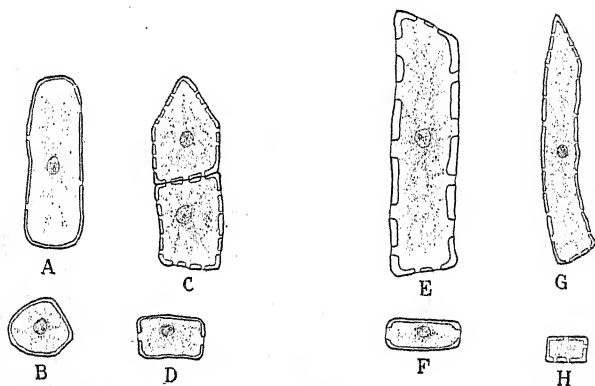


FIG. 39.—Phloem parenchyma, longitudinal and transverse sections. *A*, *B*, from *Salix nigra*. *C*, *D*, from *Robinia Pseudo-Acacia*. *E*, *F*, from *Liriodendron*. *G*, *H*, from *Pyrus Malus*.

sperms, though in pteridophytes and gymnosperms they are lacking. Functionally, the place of these cells is taken in these groups by special parenchymatous cells, which are not, however, definitely associated in position with individual sieve tubes (Chap. VIII).

Companion cells are further characterized by the presence of a protoplast with a prominent nucleus, small vacuoles, and densely granular cytoplasm. Starch is not found in them at any time. They have numerous simple pits connecting with the sieve tube with which they are associated, and very few or no pits leading to other parenchyma cells. Companion cells, judging from their position, prominent pitting with the sieve tube, type of food content, and the presence of a nucleus when the sieve tube lacks one, probably assist the sieve tube in conduction.

Phloem Fibers.—Sclerenchymatous cells are frequent in the secondary phloem of angiosperms, fibers (Fig. 38) being more common than stone cells. No mechanical elements occur in the phloem of living pteridophytes nor in that of some gymnosperms and a few woody angiosperms; that of herbaceous plants is also largely without them. The fibers of phloem differ from those of xylem chiefly in that the pits, which have small, linear or rounded openings, are always simple. The walls are in nearly all cases lignified. The long-tapering ends glide past one another in development and become interlocked, the fibers thus forming strong strands. Often they are arranged in tangential sheets or in cylinders enclosing the inner axis. They are obviously of importance as layers protective to the soft cambium region within, and also to some extent as longitudinal strengthening tissues. In some cases, as in *Dirca palustris*, they apparently are of more importance in supporting the stem than is the xylem cylinder itself.

The Term "Bast."—Because of the strength of strands of phloem fibers, these have long been used in the manufacture of cords, ropes, etc., and in the weaving of matting and cloth. Fibrous tissue used in this way has been known since early days as *bast*, or *bass*. The term was originally applied to any fibers obtained from the outer part of a plant, though a large part of such material came from the secondary phloem, as in the basswood, *Tilia*. When the secondary phloem was recognized as a tissue distinct from the cortex, the term "bast" was applied to this tissue, since it was the more common source of fibers. And in this sense, that is, as synonymous with phloem—as wood is synonymous with xylem—"bast" is still in frequent use. With the term used in this morphological sense, the fibers of the phloem became *bast fibers*. Unfortunately, however, fibers called "bast fibers," which are obtained from the outer portions of many plants, and which are used as are those of the phloem, belong in the pericycle and cortex. To these also the term "bast fibers," or simply "bast," is freely applied, a return to the older, non-technical use of "bast." Thus the term "bast" is used to such an extent without accurate botanical meaning that it seems best that it be discontinued as a technical term. Further, it is superfluous, since the terms "phloem," "phloem fibers," "pericyclic fibers," and "cortical fibers" cover with definite meanings all its uses.

Function of the Phloem.—The chief function of the phloem is conduction. According to the widely accepted opinion, the elaborated food-stuffs, both proteins and carbohydrates, move down the stem from the leaves to the trunk, roots, and other parts of the plant through this tissue. Material thus translocated may be used in respiration and growth, or stored for future use. Judging from the structure of the sieve tubes, especially from the perforation of the walls with fairly large openings, and from the fact that the contents of sieve tubes are highly protein in

nature, it is supposed that these elements are chiefly concerned with the conduction of proteins. The presence of small amounts of starch under some conditions indicates that carbohydrates may also be carried, though the starch in these cases is perhaps only the early stage of callose. It is probable that the phloem parenchyma also functions in the conduction of sugars and the more readily diffusible proteins.

Recent experiments with the ringing of woody plants seem to indicate that the phloem may also be important in upward translocation, not only of elaborated foodstuffs but of mineral nutrients as well, and that this tissue may be of more importance than the xylem in the movement of all solutes. Just how this movement takes place is no better understood than is the movement of water in the xylem.

Minor functions of the phloem are the storage of starch in the parenchyma cells and assistance in the support of the stem by various types of sclerenchyma.

Transfusion Tissue.—A peculiar type of conducting tissue, which consists largely of short tracheids with thin, cellulose walls and bordered pits or reticulate or scalariform thickenings, often accompanies typical vascular tissue in the leaves of the gymnosperms. These cells are tracheid-like in the character of their pitting and in the absence of a protoplast, but otherwise suggest elongate parenchyma cells. They lie adjacent to typical xylem at the sides of the bundle and may partly or even completely surround it. Since these cells seem to serve as conducting tissue, connecting the veins and the mesophyll of the leaves, taking the place of the usual very small branches of the veins, they form together what is called *transfusion tissue*. Though the function of this tissue is still uncertain, it undoubtedly represents modified vascular tissue.

Tissue Systems.—All the tissues of a plant which perform the same function, regardless of position or continuity in the body, are considered to form together a *tissue system*. In this sense the term is wholly a physiological one. Thus, there are found in physiological treatments of anatomy such tissue systems, as "the mechanical system," "the absorbing system," and "the storage system." The various parts of most of such systems, however, are bound together only by function; they have little or no structural or morphological unity. Continuity and similarity of nature or of origin may be lacking.

From a morphological viewpoint the grouping of tissues into tissue systems is of little importance. It is sometimes convenient, however, to designate a group of tissues in this way. In the morphological sense a tissue system must be a complex of cells extending continuously throughout the plant body or over a considerable portion thereof. It may be so simple as to consist of only one type of cell or one type of tissue, or of two or more types of tissues. Very few systems in any way structurally distinct can be distinguished, however. The older students of anatomy

distinguished an *epidermal*, or *tegumentary*, *system*; a *fundamental*, or *ground*, *system*; and a *vascular system*. The distinction of the first two systems has, as a whole, little value in present-day anatomy, and from a morphological viewpoint may well be discontinued. The vascular system is, however, a tissue system of such uniformity and continuity of structure, and of such constancy of function that it constitutes an important gross structural feature of the plant body. Xylem and phloem always make up the vascular system, and other tissues have no part in it. Hence the term is often a convenient and valuable one.

SECRETORY TISSUE

All cells directly concerned with the secretion of gums, resins, essential oils, nectar, and similar substances are together frequently referred to as secretory tissue. Such a classification is, of course, purely a physiological one, in the sense just described, as secretory cells and tissues in many cases do not have a common origin or morphological continuity. Thus, frequently secretory cells may be wholly isolated from other similar cells, being embedded in pith, xylem, phloem, cortex, or, in fact, in any tissue. On the other hand, in some cases an aggregate of secretory cells may occur and form a tissue in the strict morphological sense. Not infrequently such cells constitute a definite, organized secretory structure or gland.

Secretory Cells.—Secretory cells are of two general types: those in which the secretion formed is exuded from the secreting cell, as in glandular hairs, secretory surfaces—such as nectaries—the epithelium of resin and oil canals, etc.; and those in which the secretion formed is stored within the secretory cell. The term *excretory cells* is often applied to the first type. This type of cell is usually characterized by a protoplast with prominent, richly granular cytoplasm and a conspicuous nucleus (Figs. 40, A, B, C, E; 41, B, C, E); the secretory cell is usually large with inconspicuous cytoplasm and large lumen filled with the secretion (Figs. 40, H; 129, B). This type of cell contains in various plants many different substances, such as essential oils in *Liriodendron*, *Sassafras*, and *Zingiber*, and mucilage in many ferns. Glandular hairs often show elaborate specialization for various functions, as, for example, the stinging hairs of *Urtica* (Fig. 41, A). Such specialized hairs are often multicellular.

Glands.—Secretory cells are in many cases organized into special secreting structures commonly known as *glands*. The term “gland” is also used more loosely to indicate secreting structures of any kind, including those of all stages of complexity of organization from the solitary secretory cell to the more elaborate structures. Glands are various in function, but among the more common types are those which secrete digestive enzymes, called *digestive glands*, and those which secrete nectar, known as *nectaries* (Fig. 40, A, C). Other types are *hydathodes*, *resin ducts*, *oil ducts*, *laticiferous ducts* or *glands*, etc. Glands or ducts may have

central cavities either for storage or for conduction, in which case the cavities are either schizogenous (Chap. II), as in the resin ducts of *Pinus* (Fig. 40, *B*), or lysigenous, as in the oil sacs in the rind of the fruits of *Citrus* (Fig. 40, *F*).

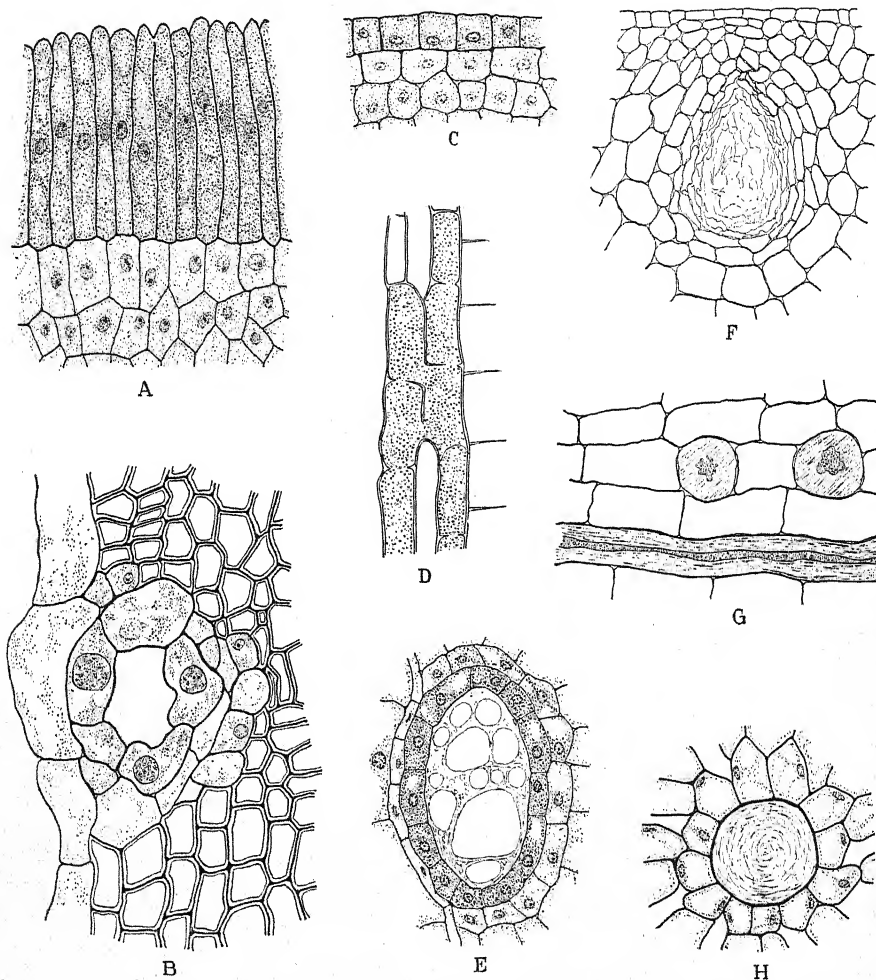


FIG. 40.—Secretory tissue. *A*, section of surface of nectary of *Euphorbia pulcherrima*. *B*, cross section of resin canal of *Pinus Strobus*. *C*, section of floral nectary of *Pyrus Malus*. *D*, latex vessel from *Tragopogon*, absorption of cross-walls in progress. *E*, cross section of oil canal of young fruit of *Angelica atropurpurea*. *F*, section of lysigenous oil cavity of rind of *Citrus sinensis*. *G*, latex cells from cortex of *Euphorbia splendens*. *H*, secretory cell of bud scale of *Liriodendron*. (*D*, after Scott.)

Digestive Glands.—In the majority of plants, enzyme secretion is not confined to specialized cells or tissues, but is a characteristic of most of the living cells. In certain so-called insectivorous and carnivorous plants, however, there are special glands which secrete protein digesting

enzymes; these enzymes act upon insects or other organisms, so that the products of digestion can be absorbed by the plant. In *Drosera*, the secretory tissue is at the tips of the leaf "hairs" or "tentacles," structures which also serve to imprison the insects. Here, in addition to the digestive enzymes, there are secreted viscid substances which hold the insects. In such plants as *Nepenthes* and *Sarracenia*, which normally have pitcher-like traps partly filled with liquid, the glands are sessile and secrete

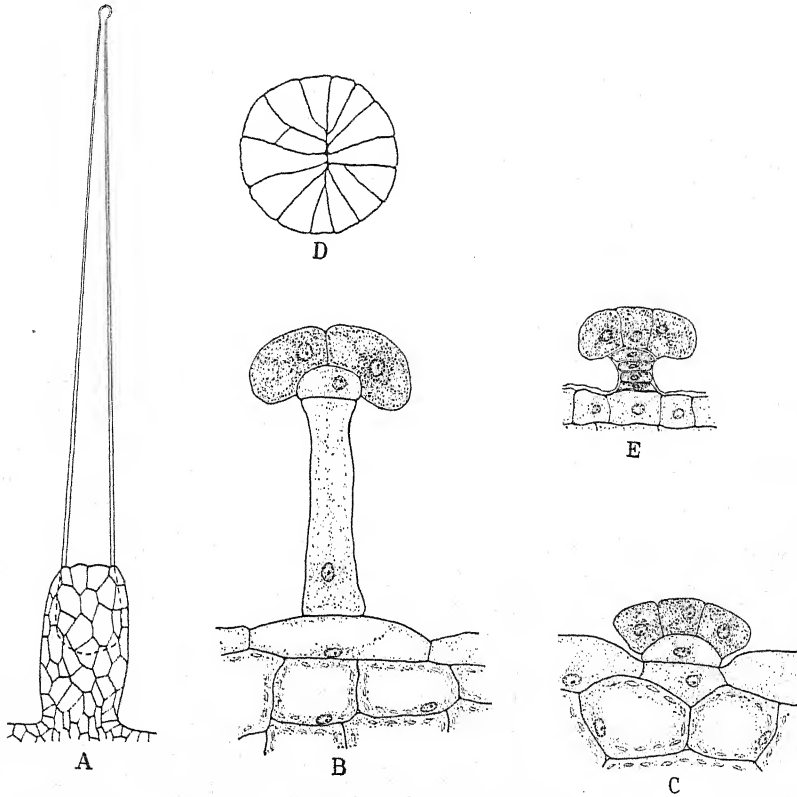


FIG. 41.—Secretory hairs. *A*, stinging hair from *Urtica gracilis*. *B*, *C*, two types of glandular hairs from leaf of *Pinguicula*. *D*, top view of *B*. *E*, glandular hair from ovary of *Gaylussacia baccata*. (The scale of *A* is much less than that of the others.)

the enzymes into the liquid from which the products of digestion are absorbed. In some other genera, for example, *Dionaea* and *Pinguicula* (Fig. 41, *B*, *C*, *D*), the glands are inactive except when stimulated by contact with animal matter. Less specialized glandular tissue of this type is found in the embryos of certain seeds, but such tissue is usually not clearly differentiated.

Nectaries.—Many entomophilous plants provide nectar for the attraction of insects. This substance is secreted by specialized cells

either on the floral parts themselves or, more rarely, on bracts or other structures outside the flower. Usually, the secretion of nectar is from specialized epidermal cells which cover certain regions of the flower, rather than from elaborate organs adapted to secretion alone. Definite and elaborate structures do, however, occur in certain families, for example, the Euphorbiaceae. In the less specialized nectaries the secreting cells are superficial upon the floral parts and in most cases closely resemble the other epidermal cells of the region but lack a cuticle (Fig. 40, C). Sometimes they are set off from the surrounding epidermal cells by a somewhat more columnar or papillose shape and by denser cytoplasm (Fig. 40, A). The nectar is exuded through the wall and exposed upon the outer or nectariferous surface. The secreting cells of stigmatic surfaces are of the same nature as those of nectaries, but are often not clearly set off from the normal epidermal cells.

Hydathodes.—Many plants possess organs for the exudation of water under conditions of low transpiration and abundant soil moisture. These are known as *hydathodes* or sometimes as *water pores* or *water stomata*. Morphologically, they are considered to be stomata which have been adapted for water secretion. Structurally, they resemble stomata very closely in many cases, but in others they may show elaborate structural specialization. Such structures do not “secrete” the fluid, but merely provide and control the openings through which it escapes. Hydathodes occur commonly at the tips of the leaves, as in grasses; at the apices of serrations on the margins of leaves; and in other positions. They are found mostly on plants of humid climates.

Resin Ducts.—In the gymnosperms generally and in a considerable number of families of the angiosperms, ducts for the secretion and conduction of resins, oils, gums, and other substances are present. In some cases, as in *Pinus*, these ducts or canals may form extensive systems extending both vertically and horizontally. On the other hand, in other plant groups the ducts may be local in occurrence and limited in extent, as in the fruits of the Umbelliferae. In *Pinus* and closely related genera, the resin ducts are schizogenous in nature, and when mature, have the structure of a tube with an epithelial lining (Figs. 40, B; 138, B). The oil ducts of the Umbelliferae (Fig. 40, E) are apparently of the same general nature. The secretory cells lining these cavities are thin-walled parenchyma with dense protoplasm. In general, these cells are elongated with the long dimension extending parallel with the long dimension of the duct. The substances secreted are various in nature, and in some cases—as, for example, the resin of *Pinus* and of *Agathis* (Kauri gum), and some essential oils—are of much economic importance.

Another type of gland is that found in the rind of the fruits of *Citrus* (Fig. 40, F). Here there is a lysigenous cavity filled with essential oil and other substances which have been formed by the disintegration of the

cells and as definite secretions before the breaking down of the tissues. The exact origin of this secretion is not well understood. These glands are the source of the essential oils of lemon and orange.

Laticiferous Ducts.—*Latex* is found in a considerable number of angiosperm families. This substance appears as a white or yellow, sometimes slightly viscous fluid which has been shown to be an emulsion of proteins, sugars, gums, alkaloids, enzymes, and other substances suspended in a matrix of watery fluid. Starch grains may be abundantly present. Just what is the function of latex is not well understood, but it is thought to be connected in some way with the nutrition of the plant. It is apparently secreted by the cells in which it is contained, and is conducted by them throughout the plant body. The latex of some plants is of great importance, especially as a source of rubber (*Hevea*, *Ficus*, etc.), chicle (*Achras*), and papain (*Carica*), as well as for other substances. Laticiferous ducts are of two types—one known as *latex vessels* and the other as *latex cells*.

Latex Vessels.—Latex vessels originate from rows of meristematic cells by the absorption, either complete or partial, of the separating walls early in the ontogeny of the vessel (Fig. 40, *D*). In the mature plant a much-branched anastomosing system is formed by the joining of more or less parallel ducts through connecting living cells and by the pushing out of lateral outgrowths into the surrounding tissue. A latex vessel thus resembles a xylem vessel to the extent that it is made up of a series of cells forming a tube by the dissolution of the end walls. Latex vessels are, however, living and coenocytic in nature. Among the families having this type of laticiferous ducts are the Papaveraceae, the Caricaceae, and the Musaceae, also the genus *Hevea* in the Euphorbiaceae.

Latex Cells.—The function and contents of the latex cell and the latex vessel are essentially the same, but the method of origin is quite different, in that the latex cell, instead of being the result of the fusion of many cells, is structurally a single cell. Latex cells occur as minute structures in the embryo of certain plants and, as the plant grows, each cell develops into a branching system ramifying throughout the entire plant body (Fig. 40, *G*). In this extraordinary method of growth the tips of the growing cells make their way through the tissues much as the hyphae of a parasitic fungus penetrate between the cells of a plant. In this type of laticiferous duct, there are no anastomoses as in the latex vessel. Latex cells are characteristic of most genera of the Euphorbiaceae and the Asclepiadaceae, as well as of other groups.

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CHAPTER V

THE PRIMARY BODY

THE PRIMARY TISSUES AND TISSUE SYSTEMS

The developing embryo of a vascular plant is very early differentiated into an axis and appendages, and the axis is in a short time differentiated into stem and root. These first-formed parts of the plant body grow rapidly and (except for the interruption brought in by the resting period of seeds) soon become mature. The root and stem remain meristematic at the tip, but the appendages, which are of limited growth, become mature throughout. Exceptions to the continued growth of the axis occur, for example, in flowers, thorns, and specialized roots; but normally the apical growth of the axis is unlimited, and by its activity the root and stem are increased in length, and the lateral structures, both the appendages of various ranks and the branches of the stem, are added. Branches of the root develop in a different way (Chap. X), and adventitious roots and stems develop nearly always from new meristems formed in permanent or in traumatic tissue.

Apical meristems, together in some cases with intercalary meristems, thus build up the new portions of the stem and root and form the appendages. These parts of the body are structurally and functionally complete, at least temporarily, and constitute the primary body of the plant. Secondary growth may be added later, but the primary body is complete in itself. Thus all the fundamental tissues and body parts are present when primary growth is completed. These are, in the axis, the central cylinder with its xylem, phloem, pith, pericycle, and endodermis; the cortex; the epidermis; and, in the leaf, the corresponding regions and tissues. These parts show great variety of structure in different plants and in different parts of the same plant; that is, the vascular tissues of the central cylinder are arranged in one plant in a way entirely different from that in another plant, and at a node are differently placed than in the adjacent internodes. Such variations of grosser general structure are discussed later in the chapter; the present discussion is given to the histological and anatomical features of the various primary tissues and regions.

Ontogeny of the Axis.—At or near the apex of the axis lie the apical cells, the persistent initiating cells which develop the primordia of every region (Fig. 27). The cells cut off by the apical cells divide rapidly, forming a multitude of cells similar in every way. The region made up

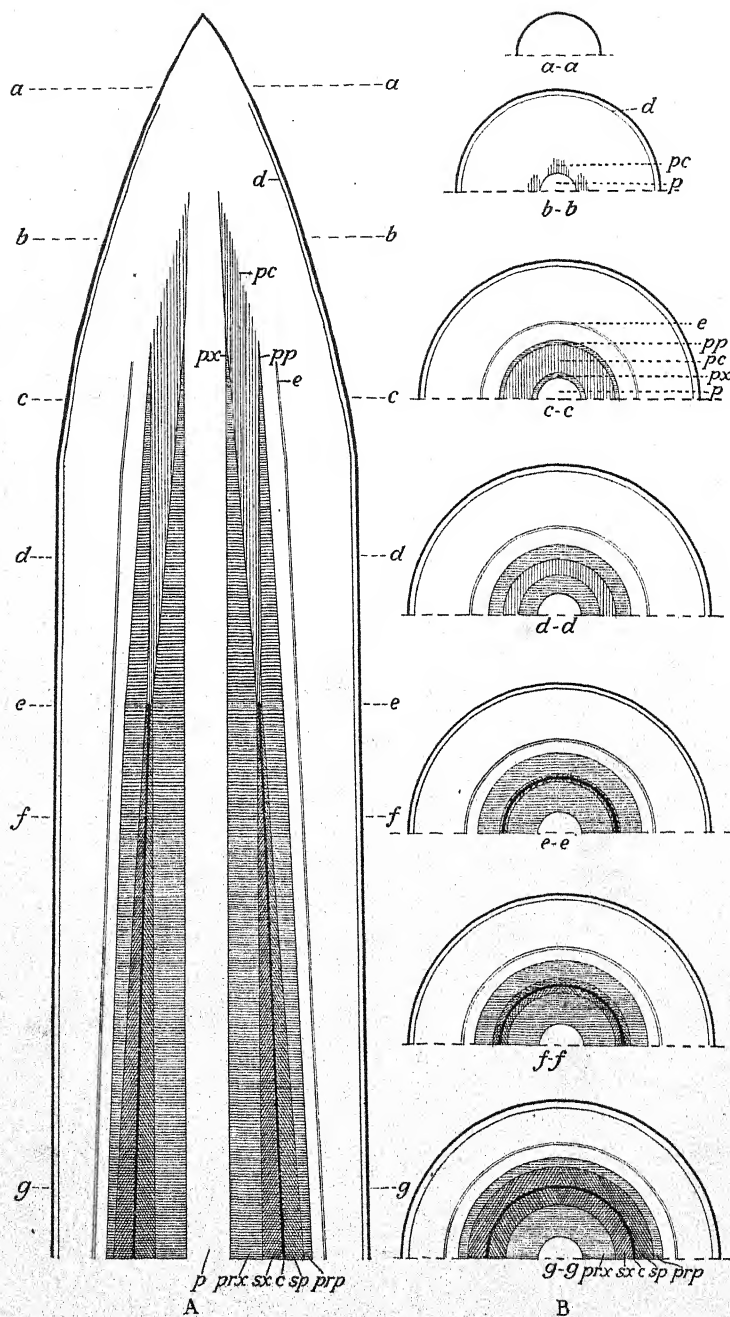


FIG. 42.—(Legend, foot of p. 85.)

of these—a region in which growth takes place largely by increase in number of cells through division, rather than by increase in cell size—is the *promeristem* (Figs. 25, 28, 42). The cells of the promeristem differentiate as they become older, showing evidence in changes of size, shape, wall thickness, and character, etc., of the various different cell types into which they are destined to develop. With this step the promeristem passes over into meristem in which a certain amount of cell differentiation is evident. This latter type of meristem in turn passes over into permanent tissue. Thus, there is progressive development in any group of cells from promeristem cells to permanent tissue through phases of meristem change. Thus, if a group of cells is viewed at different periods in its development, it will be found in the various stages mentioned. And, since the growth of the axis is apical, and since the various structural features of the axis are likewise continuously formed, there are found at various distances back from the apex, stages of development representative of the stages through which a given group of cells will pass as the cells become older. In other words, the development through which a given part of the axis passes, over a period of time from its beginning until it reaches maturity, may be found at any one time in different levels of the axis, progressively farther and farther from the apex. Thus, development as seen in spatial extent supplies the story of development in time. (The differences in nodal and internodal structure are here neglected.) It is thus evident that a series of cross sections of the axis taken in turn farther and farther away from the apex give the history of development of a cross-sectional area. Such a series is shown in Fig. 42, which also shows in longitudinal section progressive differentiation without break in continuity, though, of course, only in the plane of section. In order that a comprehension of primary structure may be had, it is essential that this gradual differentiation in time be understood, as well as the fact that this may be seen expressed in space in the longitudinal extent of the growing axis tip.

The transition from meristem to permanent tissue does not take place simultaneously throughout a given level in the axis; there is an overlapping of the meristem upon the mature tissues. For example, Fig. 42, *c-c* shows a stage where the pith and a part of the vascular tissues are

FIG. 42.—Diagrams showing development of the axis. *A*, longitudinal section of tip of elongating axis. *a-a* to *g-g*, cross sections of the axis at levels *a-a*, *b-b*, etc. At *a-a*, the entire axis is promeristem. At *b-b* the dermatogen (*d*), procambium (*pc*), and pith (*p*) are in early stages of development. At *c-c*, the procambium has increased in amount, forming a complete cylinder; the outermost and innermost procambium has become protophloem (*pp*) and protoxylem (*px*); the endodermis (*e*) is evident. At *d-d*, the procambium is less in amount, large portions of this tissue adjacent to the protophloem and protoxylem having become phloem and xylem. At *e-e*, the remaining layer of procambium has become the cambium, and has formed the first secondary phloem (*sp*) and secondary xylem (*sz*) cells. At *f-f*, the secondary tissues are increased in amount; the primary phloem (*prp*) is reduced by crushing; the cambium has moved outward. At *g-g*, further secondary growth has occurred.

mature. Other cells beside or around these are immature, being in the stage of procambium or even of promeristem. In a similar way, primary growth of a given section of the axis is not completed throughout the region in question before secondary growth begins; that is, there is here again an overlapping in development. It is thus impossible definitely to delimit by transverse planes the promeristem or the primary tips; this may, however, be done approximately.

Appendages consist chiefly of primary tissues. Leaves may be wholly primary; often the larger veins possess secondary growth. The ontogeny of the leaf is discussed in Chap. XII.

PRIMARY VASCULAR TISSUE

The Procambium.—In the differentiation of the axis and of the leaf out of promeristematic tissue the presence of a dermatogen is in most

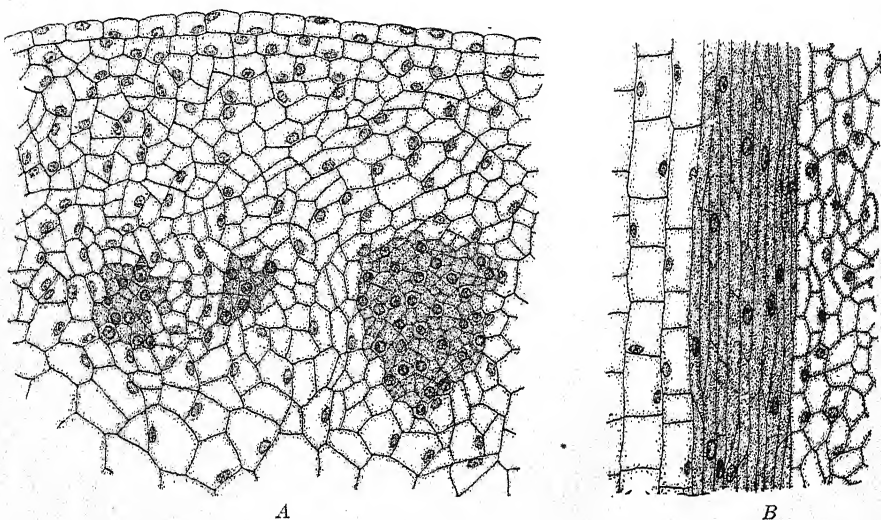


FIG. 43.—Procambium in cross and longitudinal section in stem tip of *Linum usitatissimum*. The procambium cells have smaller transverse diameter, are elongate, and have more dense cytoplasm.

cases the first evidence of the structural complexity of the mature organ. The first cells to become mature, however, either in leaf or in axis, belong to the vascular tissue. In the promeristem, where all cells are essentially isodiametric and alike, there early appear groups or strands of narrow, elongate, densely protoplasmic cells (Fig. 43). This tissue is destined to give rise to xylem and phloem and is known as *procambium*. (The term “procambium” is here used as indicating that meristematic tissue which gives rise to the morphological vascular units, and not in the physiological sense of application to any elongate cells which are cambium-like in shape and activity.) The procambium foreshadows, as

specialization begins in the promeristem, the position, the direction of development in relation to the center of the axis, and, to a certain extent, the amount of primary vascular tissue in the mature organ. (The first procambium of an axis appears usually in definite, isolated strands. The cells of these strands at a given place or level in an organ do not mature simultaneously from promeristem, but develop in order in definite, restricted directions from a fixed point of beginning. By the continued addition of cells from the adjacent promeristem the procambial strands, at first very slender, become much increased in size. Such enlargement is often so great that the strands fuse and form a solid central core or a hollow cylinder (Fig. 44). While more and more procambium is developing from promeristem, the first-formed cells mature into xylem and phloem cells. Thus there may be found in the region of a developing

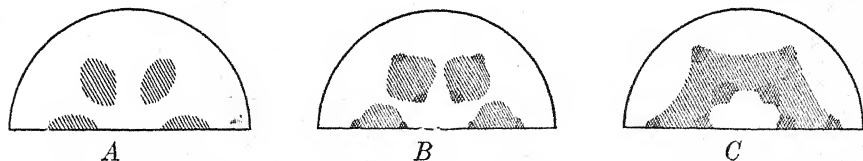


FIG. 44.—Diagrams showing stages in the development of a procambium cylinder from promeristem. *A*, the first procambium has appeared in the promeristem in the form of strands. *B*, the strands of procambium have increased in diameter, approaching one another, and the oldest portions (on the outside and the inside) have become phloem and xylem. *C*, the strands of procambium have united laterally, and more procambium has matured as phloem and xylem. In a later stage all procambium will have become vascular tissue, forming a primary vascular cylinder.

procambial strand all stages from promeristem to mature vascular tissue. Indeed, when some cells have already become xylem and phloem, other promeristem cells, of like destiny, may as yet show little or no indication of change.

Just as the cells of a procambial group are thus formed progressively from promeristem, so cells of xylem and phloem mature in like manner from the procambium. Definiteness and uniformity of order of development transversely in an organ are important characteristic features of primary vascular tissue. The points of beginning of this development are constant in position in certain organs and in certain plant groups. They are commonly situated on the edge of the procambial group of cells. Since vascular tissue consists in nearly all cases of both xylem and phloem, the procambium is made up of two parts, one of which develops xylem and the other phloem. These regions are not, however, histologically distinct in early stages. Only when the first cells of xylem and phloem approach maturity can the position of the respective tissues be determined with certainty. The portions of the procambium which form the first xylem and those which form the first phloem are situated well apart, either radially, as in stems and leaves, or tangentially, as in roots.

Centripetal and Centrifugal Growth.—The development of mature vascular cells from procambium progressively from the point of beginning toward the center of the axis is known as *centripetal growth* (Fig. 45, *B*), and that away from the center of the axis, *centrifugal growth* (Fig. 45, *A*). These terms apply to the order of maturation of the elements radially. Development in a longitudinal direction, is, of course, in general, *acropetal*; *basipetal* development may occur in the bundles of leaves, in leaf traces, and in stems where intercalary meristems occur, and where, in apical growth, nodal regions mature before internodal. The development of phloem is probably always centripetal, whereas that of xylem is sometimes centripetal and sometimes centrifugal. Less commonly, the first-formed cells are situated, not at the edge of the procambium, but nearer the center, and development is then both toward and away from the center of the axis (Fig. 45, *C*). In xylem when the development is toward the

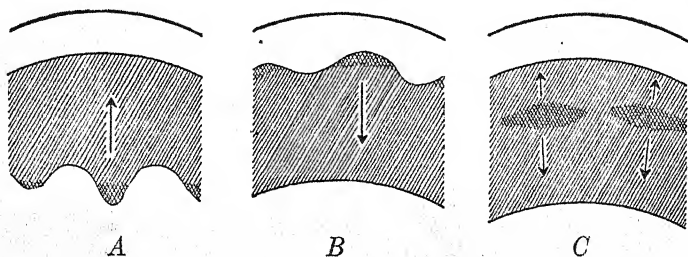


FIG. 45—Diagrams showing order of development of vascular tissue transversely in an organ. *A*, centrifugal. *B*, centripetal. *C*, both centrifugal and centripetal. These diagrams may also illustrate types of xylem from the standpoint of order of development: *A*, endarch; *B*, exarch; *C*, mesarch (see p. 95).

center of the axis, *centripetal xylem* is formed, and the xylem group or strand is said to be *exarch* (Fig. 45, *B*); when it is *away from* the center of the axis, *centrifugal xylem* is formed and the xylem unit is said to be *endarch* (Fig. 45, *A*). When development is such that both centripetal and centrifugal xylem are formed—even though the amount of one type be very small—the xylem is *mesarch* (Fig. 45, *C*). Development must always be considered as *relative to the center of the axis*, not to the center of the vascular bundle in question. It should be borne in mind also that the terms “centripetal growth” and “centrifugal growth” refer only to sequence of appearance and of maturation of procambium cells in definite directions and do not imply growth in the sense of successive new-cell formation. Exarch, endarch, and mesarch xylem characterize definite organs or parts of organs, and are restricted more or less in their distribution in the larger plant groups. For example, the root is always exarch; the stem of seed plants is endarch; the axis of the clubmosses is exarch; mesarch xylem is common in the ferns and infrequent elsewhere. Thus the distinction of xylem in this way is of much morphological and phylogenetic importance.

Protophloem and Protoxylem.—The first cells of the phloem to mature are known as the *protophloem*, those of the xylem, the *protoxylem*. These cells differ markedly from later formed cells of the same tissues in cell type; in size, being narrow and slender; and, in the case of xylem cells, in

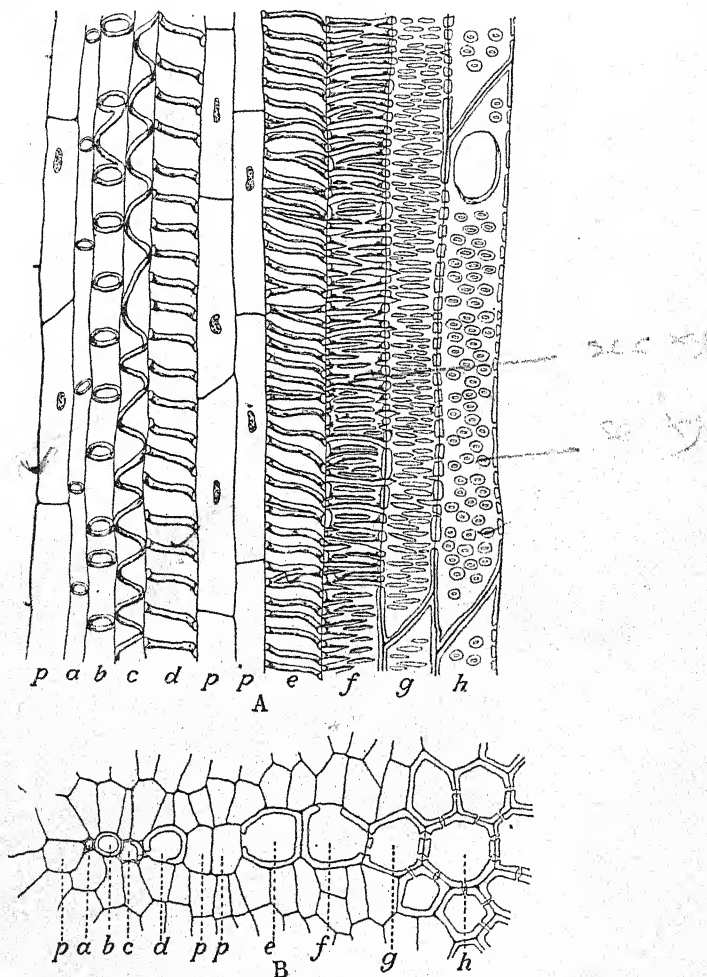


FIG. 46.—Protoxylem and metaxylem in transverse (B) and longitudinal (A) section in *Lobelia*. *a*, *b*, annular elements. *c*, *d*, *e*, spiral elements. *f*, scalariform element. *g*, scalariform-reticulate element. *h*, pitted vessel. *p*, parenchyma cell.

the character of the wall. Since they are formed very early in the ontogeny of the tissue in which they lie, they are subject to tissue stresses due to increase in diameter, and particularly to increase in length. To these stresses the surrounding meristematic cells accommodate themselves by cell division and by increase in size; but the cells of the proto-

phloem and the protoxylem are mature and no longer subject to growth changes. In the region in which protophloem and protoxylem lie, the greatest change occurring is increase in length. The stresses brought about by this elongation tend to stretch the already matured cells. To such longitudinal stretching protoxylem and protophloem cells are, to a limited extent, adaptable. The cells are long and slender with walls which are thin and of cellulose, reinforced in protoxylem by bands of lignified secondary wall (Fig. 46). These bands, in the form of rings and spirals prevent to some extent the collapse of the thin, plastic walls and the consequent closure of the lumen.

To those phloem and xylem cells which are thus capable of stretching, the terms "protophloem" and "protoxylem" are restricted. The parts of phloem and xylem which are not stretched by elongation of the region in which they lie are known as *metaphloem* and *metaxylem* respectively. Thus primary phloem consists of protophloem and metaphloem; primary xylem, of protoxylem and metaxylem. In secondary phloem and secondary xylem no protoxylem and protophloem exist, for secondary tissues develop only after elongation ceases. A strand of xylem may consist wholly of protoxylem—the condition in most very small vascular bundles—or wholly of metaxylem, as in some slow-growing roots and rhizomes, but commonly both types of xylem are present, the proportions varying with the plant, the organ, and the rapidity of growth of the region in question.

It is obvious that in exarch xylem the metaxylem lies internal to the protoxylem (Fig. 45, *B*, the protoxylem heavily shaded); in endarch xylem external to the protoxylem (Fig. 45, *A*); and in mesarch xylem both toward the inside and toward the outside of the protoxylem (Fig. 45, *C*).

Structure of Primary Phloem.—Structurally, protophloem is not complex. In many cases—and perhaps always—it consists of phloem parenchyma only, sieve tubes being absent. The slender parenchyma cells of protophloem differ so slightly from the procambium cells from which they are derived, and from small sieve tubes, that their identity can be established only with much difficulty. Physiologically, they function but a very short time, since they are soon weakened by elongation, and crushed and flattened by increase in diameter due to growth of cells in the inner part of the axis. The remnants of the cells are in many cases rapidly absorbed, so that soon after the cells mature all evidence of their existence may be lost. Morphologically also, the position and the character of the protophloem seem to be of little importance.

The metaphloem, on the other hand, is a complex tissue with well-developed cells of all types—sieve tubes, companion cells, parenchyma cells, and sclerenchyma in the form of fibers (though fibers as a constituent of primary phloem are not abundant and in many cases are wanting).

The various cells types are essentially the same as those of the secondary phloem of the same plant.

Like the protophloem, the metaphloem may be early crushed by the development of secondary tissues beneath. In woody plants the soft cells of the primary phloem are often completely destroyed within a short time after maturing, because of secondary growth beneath them. The remnants of the flattened cells may exist for some time or be quickly absorbed like those of the protophloem.

Primary phloem is thus of little functional importance where secondary phloem is developed in considerable amount. Where, however, little nor no secondary phloem is formed, the primary phloem persists throughout the life of the organ, and may be of the greatest importance physiologically. Structurally, such phloem is highly specialized, consisting usually only of sieve tubes of the highest type and their accompanying companion cells. Such is the condition in the phloem of most monocotyledons, and of such dicotyledons as *Cucurbita*, *Ranunculus*, and *Podophyllum*. In these genera the phloem of the bundles is in part secondary, but the primary and secondary phloem do not differ histologically to any extent. In other herbaceous plants, such as *Solanum*, *Aster*, and *Lobelia*, where definite cylinders of secondary vascular tissue occur, but where the amount of secondary phloem is small, the primary phloem persists as functioning tissue through the life of the stem. In such forms the sieve tubes and companion cells often occur in small groups and are remarkable for their small size. An entire group may be of no greater diameter than one of the adjacent parenchyma cells (Fig. 115). The discussion of the histology of secondary phloem (Chap. VIII) may be applied to such primary phloem. ✓

Structure of Primary Xylem.—In contrast with protophloem, protoxylem may contain several kinds of cells. These are tracheids, vessels of one or more types, and parenchyma cells. Fibers are absent. The parenchyma cells make up a large proportion of the first-formed tissue. The term "protoxylem" is, unfortunately, often used in the physiological sense, referring only to the more or less scattered tracheids and vessels. The term is applied in its best usage, however, to the continuous tissue, distinct as a morphological unit.

Conducting Elements of the Protoxylem.—The water-conducting cells of the protoxylem are the characteristic cells of this tissue because of the peculiar adaptation of their walls to the stretching which they normally undergo. The thin, plastic, primary walls of these empty cells are strengthened by the addition of a lignified secondary wall in the form of narrow rings and spiral bands. These bands apparently help to keep the conducting channels open during the elongation of the cells. The first-formed protoxylem cells have small amounts of secondary wall in the form of rings spaced at intervals along the cell (Fig. 46, *a*, *b*). Such cells

are called *annular cells*, or *annular elements*. (The term "element" is often used in speaking of cells of the protoxylem when the cells in question may be either tracheids or vessels.) Cells formed a little later than annular cells possess secondary walls in the form of spiral bands; such cells are called *spiral cells*, or *spiral elements* (Fig. 46, c, d, e). The flatness of the coils and, to some extent, the number of the bands increase in the cells formed successively later and later. The proportionate amount of secondary wall thus increases in the successively formed cells. The first-formed cells are subjected to excessive amount of elongation, those formed later and later to less and less. Structurally, the cells formed at any given period are adapted to the amounts of elongation occurring after their formation. Annular cells may be stretched to a greater extent than spiral cells; cells with steep spiral coils more readily than those with flat coils; those with one spiral more freely than those with several. Where the structure of the secondary wall suggests a spiral lying in flat coils, the coils fused at the corners of the cell, or where a more definitely ladder-like appearance is produced by transverse bar-like thickenings running from corner to corner, the cell is known as *scalariform* (Fig. 46, f). (The scalariform cell of protoxylem is best called a scalariform protoxylem cell, since the term "scalariform cell" is a general term and may refer to a scalariform-pitted tracheid or to a scalariform (pored) vessel. A scalariform protoxylem cell may, of course, be also a scalariform vessel.)

Metaxylem Elements.—The scalariform protoxylem cell is, obviously, capable of little if any stretching. Where the bands of secondary wall are more extensively and less uniformly tied together, forming a network of secondary thickening, a *reticulate cell* is formed (Fig. 46, g). Where the secondary wall is still more extensive and the thin spots in the wall are definite and uniform in size and shape, the cell is *pitted* (Fig. 46, h). Reticulate and pitted cells cannot be stretched. Primary xylem consisting of these cells is, therefore, metaxylem. Scalariform cells fall on the line between protoxylem and metaxylem, some of them being capable of slight stretching, but most of them rigid. It should be borne in mind that no sharp line separates any one type of cell from the next type, or protoxylem from metaxylem.

Protoxylem Vessels.—The water-conducting cells of protoxylem may be either tracheids, or vessels. They are undoubtedly tracheids in pteridophytes and gymnosperms and in the less highly specialized angiosperms. In other flowering plants both kinds of cells occur together, and in herbaceous forms and some woody forms the water-conducting cells of the protoxylem are largely vessels. Protoxylem cells are made abnormally long by stretching, and the end walls are not readily seen in section. It is in part due to the vessel-like appearance thus given to any water-conducting cell of the protoxylem that the term "protoxylem

vessel" has been applied to all such cells regardless of their tracheidal or tracheal nature; but this incorrect usage is probably due more to a retention of the idea of the seventeenth and eighteenth centuries that the animal-trachea-like appearance of spiral cells indicates a conducting tube of indefinite length. The use of the term "vessel," or "trachea," in this sense is responsible for the incorrect opinion that "vessels occur in the gymnosperms only in the protoxylem." It often cannot be readily determined whether a given cell of the protoxylem is a vessel or a tracheid; such a cell may then be called, for example, "an annular cell," or "an annular element;" it should not be called a vessel unless there is proof of the perforation of its end walls.

Proportion and Arrangement of Types of Protoxylem Elements.—In the protoxylem of a given vascular bundle, annular, spiral, and scalariform cells may all exist, and each in any proportion; or one or two of the types may be lacking. Spiral cells, however, especially those with closely coiled bands, constitute a large proportion of most protoxylem strands. Where growth of the axis is rapid, a high percentage of annular elements is found; where slow, very few or no such cells occur. As a strand of protoxylem forms, not only is the wall of the successively formed cells of different character, but the cells themselves become each somewhat larger than the preceding ones. The order of development may thus usually be determined, when several or all cells are mature, on the basis of size alone. Often, however, there are variations and exceptions to the sequence in size, but the structure of the wall is constant in its relation to order of development. Protoxylem cells are arranged irregularly, in contrast with the cells of secondary xylem. In many herbaceous angiosperms, however, and also in certain woody forms where the water-conducting cells of the primary xylem are chiefly vessels, these cells lie in radial rows, thus simulating secondary tissues. It is characteristic of nearly all primary tissues that their cells have little or no regularity of arrangement.

Elongation of Protophloem and Protoxylem.—Though protophloem and protoxylem are structurally adapted to stretching, and the earliest-formed cells especially so, the elongation to which they are subjected is in many cases so great that their plastic capacity is surpassed and they are ruptured. The protophloem cells are in many cases rapidly absorbed after destruction, but the torn remains of the protoxylem tracheids and vessels persist permanently. Annular cells, being the first cells formed, are most frequently destroyed. Probably nearly all annular cells which are not destroyed are so distorted soon after their formation as to become non-functional. The stretching of these cells at first separates the supporting rings, and the thin, distended wall between them soon sags or collapses. The further pulling of the walls tilts the rings and turns them up on edge (Fig. 47, B). Still further elongation fragments the

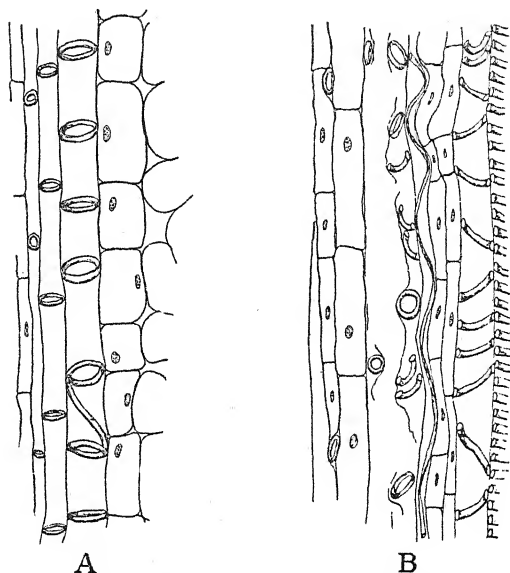


FIG. 47.—Protoxylem in longitudinal section. *A*, from fruit of *Arisaema*; the elements are all annular and there has been little stretching and no rupture. *B*, from stem of *Equisetum*; there has been extensive stretching of annular and spiral cells, with rupture of the former and the formation of a protoxylem lacuna.

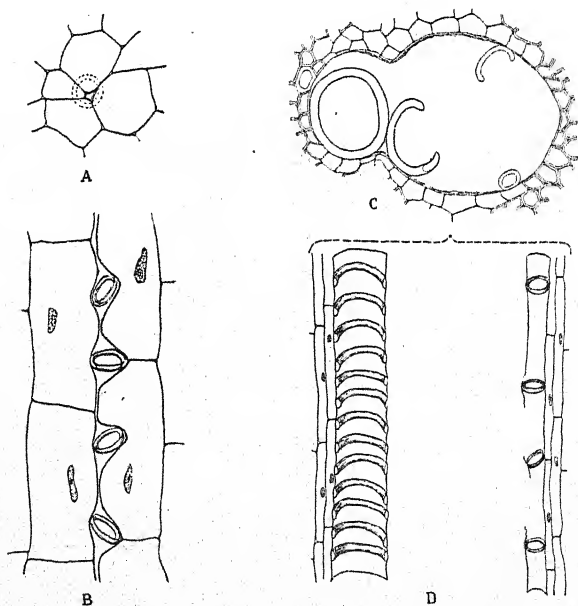


FIG. 48.—Protoxylem in transverse and longitudinal section, showing behavior of surrounding tissue. *A*, *B*, from *Lobelia*, showing a stretched annular element, the primary wall collapsed between the rings, the adjacent parenchyma cells pressing into the spaces; in cross section the space originally occupied by the cell nearly filled in. *C*, *D*, from *Zea*, the surrounding parenchyma pulled away from the protoxylem elements, leaving a large lacuna.

cells, and isolated rings of secondary wall, often with pieces of the primary wall attached, are to be found where the cells have been destroyed. In spiral cells the spiral is pulled out so that it becomes steeply wound or is even straightened out (Fig. 47, *B*). In such cases also the primary wall collapses.

Protoxylem Lacunae.—Where a number of protoxylem cells lying together have been thus destroyed, a canal-like cavity, known as a *protoxylem lacuna*, may be formed (Fig. 47, *B*). In some instances such an intercellular space is much enlarged by the pulling away of the surrounding parenchyma cells. Exaggerated protoxylem lacunae formed in this way are found in many herbaceous plants, and especially in the monocotyledons (Fig. 48, *C*, *D*) and the horsetails (*Equisetum*). On the other hand, the growth of tissues surrounding the developing bundle at the time of the rupture of the protoxylem cells may be such that no lacuna is formed, but the surrounding parenchyma cells press in upon the flattening xylem cells and fill up the space occupied by them (Figs. 47, *B*, left annular element; 48, *A*, *B*). In annular or loosely spiral cells, parenchyma cells thus may be found pushing into the hollows formed by the sagging wall, or, tylosis-like, into the lumen when the wall is ruptured. Rings from annular cells sometimes become pressed, upright, between parenchyma cells (Fig. 47, *B*). In such cases the position of the first-formed protoxylem cells may be difficult to ascertain in transverse sections.

Primary Xylem Types.—The type of primary xylem—exarch, endarch, or mesarch (Fig. 45)—is determined by the position of the protoxylem in relation to the metaxylem; or, in case the primary xylem consists only of protoxylem, by the determination of the position of the first-formed cells. This may be detected by the location of the protoxylem lacuna, if such is present; or, where the tissue has closed in upon the torn or flattened cells, by the disturbance in normal cell arrangement and by the fragments of the destroyed cells. For the determination of xylem type, the study of longitudinal sections is sometimes necessary, since in cross sections annular cells may be with difficulty separated from spiral cells, and the first-formed annular cells may be obliterated at certain levels.

It cannot be too emphatically stated that the different types of protoxylem tracheids and vessels are formed at successively later and later stages in the ontogeny of the tissue. No cell, once mature, changes its character; an annular cell does not become a spiral cell, nor a spiral cell a scalariform cell. The increasing amounts of secondary wall present are found in cells successively formed.

The Term "Vascular Bundle."—The term *vascular bundle* is applied to a strand-like portion of the conducting system of a plant. Such a bundle consists fundamentally of primary tissues; with these, secondary tissues may be present. Small bundles—bundle ends, and the slender bundles of leaves, fruits, etc.—are wholly primary. Larger bundles,

such as those of monocotyledonous stems, may also be wholly of primary development; and those of many herbaceous dicotyledons are largely primary in nature. In these bundles the xylem and phloem are highly specialized, the conducting cells being of high type and reduced in number, and supporting cells few or lacking. In such cases protection and support are often given to the soft or weak conducting tissues, and support is given to the organ in which the strands lie, by sheaths of fibers which more or less completely surround the strand of conducting cells. Because of the frequent presence of these fibrous sheaths with the conducting cells, the fibers were at one time supposed to constitute a part of the bundle, both morphologically and physiologically, and the bundle was, therefore, called a *fibrovascular bundle*. It has long been clear, however, that the function of the bundle is primarily conduction, and that the "mechanical tissue" of an axis is not necessarily related in position to the bundle; also that the fibrous tissue adjacent to the conducting strand is morphologically not a part of the vascular tissue. Hence, the much better term *vascular bundle* has been in recent years substituted for *fibrovascular bundle*. The new term has not, however, wholly replaced the older and less accurate term. The vascular bundle is further discussed in Chap. XI).

Types of Vascular Bundles.—It is characteristic of vascular tissue that phloem or xylem is rarely found alone; a bundle usually consists of both

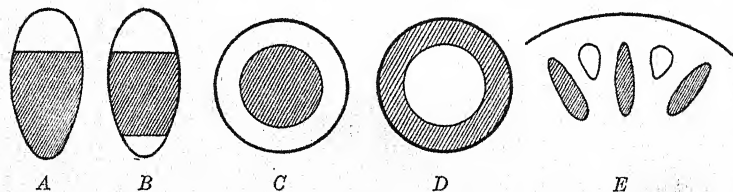


FIG. 49.—Diagrams showing types of arrangement of xylem and phloem with relation to each other. (The xylem is shaded, the phloem unshaded.) A, collateral bundle. B, bicollateral bundle. C, amphicribal bundle. D, amphivasal bundle. E, radial arrangement.

of these types of conducting tissue. When together, xylem and phloem show several types of arrangement with each other in the bundle. These fall into three general classes: first, those in which the xylem and the phloem lie radially side by side; second, those in which one type of tissue surrounds, or ensheaths, the other; third, those in which the two types of tissue are separated from one another. In the first group are *collateral bundles* (Figs. 49, A; 116, A, D; 117), the phloem lying beside the xylem and external to it; and *bicollateral bundles* which are merely collateral bundles with phloem on the inside of the xylem also (Figs. 49, B; 115). Bundles of the second group are known as *concentric bundles*, the type in which the phloem surrounds the xylem being *amphicribal* (Figs. 49, C; 116, B), and that where the xylem surrounds the phloem, *amphivasal* (Figs. 49, D; 116, C). The term "concentric bundle" is often loosely used to

indicate an amphicribal bundle. This is due to the fact that the amphivasal type of concentric bundle is uncommon, and "concentric" is believed to be sufficiently specific. Concentric should be used only as a general descriptive term covering both amphicribal and amphivasal conditions. The arrangement of the tissues in the third group is such that no definite bundles are formed. Strands of xylem and of phloem lie on different radii of an axis, separated by non-conducting tissue (Figs. 49, *E*; 105). These strands are commonly said to constitute *radial bundles*. Since, however, no definite bundles exist—unless each strand be considered a bundle—and the xylem strands are often not independent but are united in a central core, it is better to call such a condition in the primary xylem and phloem *radial arrangement*. The term "radial bundle" goes back to the period before the proposal of the stelar theory; the stele of a root then constituted one bundle, radial in structure. Unfortunately, the term is still occasionally applied to the primary vascular structure of roots. The terms "exarch," "endarch," and "mesarch" are sometimes also applied, descriptively, to bundles; in such cases they merely indicate that the xylem of the bundle is of the stated type.

Occurrence of Bundle Types.—The collateral bundle is the common type of bundle and is characteristic of the stems and leaves of angiosperms and of most gymnosperms. The bicollateral bundle is uncommon, occurring in those angiosperms which possess internal phloem in their steles, as, for example, the Cucurbitaceae. Amphicribal bundles are common in the ferns; and small bundles, such as the bundles in floral parts, ovule traces, and small leaf-trace bundles are commonly of this type. Amphivasal bundles are rather rare. They occur chiefly in the monocotyledons, and there, largely in nodal regions and in rhizomes. The radial arrangement of primary vascular tissue is characteristic of roots, where it is always present, and does not occur elsewhere.

Vascular bundles are to be thought of as parts of a unit vascular system, not as fundamental structural units; in the axis they are more or less isolated segments of a stelar column or cylinder.

THE PITH

The pith is a roughly cylindrical body of tissue in the center of the axis, enclosed by the vascular tissues. Its outer surface is furrowed more or less deeply by the inwardly projecting strands of protoxylem, and ridged in some cases by ray-like extensions between bundles, and by projections where its tissues extend out through leaf and branch gaps. The number, prominence, and arrangement of these furrows and ridges depends upon the skeletal plan of the plant in question, and upon other features. The pith was for a long time known as the *medulla*, but this

Latin name has become obsolete. As a descriptive word, the name still persists, as in "medullary ray" and "medullary spot."

Structure of the Pith.—Histologically, the pith is made up of rather uniform tissue, chiefly parenchymatous, in which the cells are arranged rather loosely, often with pronounced intercellular spaces, and in some forms tending to be in longitudinal rows (Figs. 30, *A, C, D, E, F*; 112). In shape, the cells of the pith vary greatly, but they are mostly rounded, isodiametric, or cylindrical, with thin, cellulose walls. Not uncommonly, thick-walled, lignified parenchyma cells and stone cells are also present, often arranged in groups forming plates or diaphragms of firm tissue. Fibers occur only rarely and then in the peripheral portions where they probably are associated morphologically with primary vascular tissue, especially with internal phloem. When the pith is developing, all the cells are active and in leafy shoots may even contain chlorophyll; but when the region is mature, the cells become less active and all may have lost their protoplasts, or living and dead cells may be present in any proportion. The proportions vary in different parts of a plant, such as the node and the internode, and in different species. Usually, the smaller cells and those nearer the vascular tissue remain alive. In some cases these small living cells form a fairly definite pattern with the non-living cells. In woody plants the living cells of the pith serve as storage cells in resting periods, becoming filled with starch and fatty substances.

In kinds of cells, intercellular spaces, secretory tissues, etc., the pith is usually closely similar to the cortex of the same plant. Protective, supportive, and photosynthetic cells are, however, scarce or lacking in the pith.

In the ontogeny of the stem, the pith cells in many cases mature very early, and no further growth occurs. The surrounding tissues are meristematic and continue to elongate. Thus, the pith may be torn apart longitudinally to a greater or less extent. If marked radial increase is taking place at the same time, a prominent "hollow pith" is formed, with the broken cell walls lining the cavity (Fig. 113, *C*). This condition is common among herbs but rare in woody plants. Where the destruction is less extensive, cavities or canals of various extent and shape are formed. The presence of transverse layers of more resistant cells often brings about the development of a "diaphragmed pith." The diaphragmed condition may in other cases result from a slight increase in length of the axis after the pith has become mature. Nodal diaphragms are due to the presence of thicker-walled cells at the node, or to the very slight elongation of the nodal regions as contrasted with the extensive growth of the internode (the expansion of a bud being due in large degree to the development of internodes).

The Medullary Sheath.—The peripheral layers of the pith consist of smaller cells, usually thicker-walled, more closely packed, and more

richly protoplasmic. Though this region merges into the central part, it is often distinguished as the *medullary sheath*, or *perimedullary zone*. If an inner endodermis is present, the medullary sheath is separated from the pith proper by this layer. It is in such cases clear that the medullary sheath constitutes, in part, an inner pericycle. Its outermost parts represent the parenchyma of the primary xylem, since the groups of protoxylem tracheids and vessels project into the sheath; and when internal phloem is present, the sieve-tube clusters lie near the middle of the sheath. This layer is not, therefore, morphologically, a part of the pith.

The medullary sheath is differentiated in various ways: its cells may remain typically parenchymatous, as in many *Chenopodiaceae*, *Boraginaceae*, and *Euphorbiaceae*; or become strongly lignified, as in members of the *Umbelliferae* and *Compositae*; or both parenchymatous and sclerenchymatous cells may be present. Fibers, however, occur but rarely, and then chiefly in connection with internal phloem.

The Pith of Roots.—Roots characteristically lack a pith, but where such a core is present, it is similar in cell structure to that of the stem of the plant. The pith of roots tends to be more homogeneous, however, and does not break down. It is more nearly cylindrical, since the primary xylem points do not project into it, and since there are no gaps in the vascular cylinder.

Duration of the Pith.—The pith persists indefinitely in nearly all plants. In woody stems the changes taking place in heartwood formation of the first annual rings affect the pith cells in a similar way. But until this stage is reached some of the pith cells remain alive in most woody plants. In other forms, however, the pith very early becomes wholly non-living. The pith is not crushed by the crowding in upon it of the vascular bundles as secondary growth takes place. Only in a few woody vines of anomalous stem structure, such as *Aristolochia*, is there found this peculiar condition of crushing during secondary growth. Further, no growth or structural change of cell wall occurs after primary growth of the axis is complete. Therefore, the pith is present in old stems—tree trunks, etc.—in size, shape, and structure exactly as it was in the young twig when secondary growth began. Only in lack of protoplasts and in chemical nature is it different.

THE PERICYCLE

The pericycle is a thin cylinder of tissue sheathing the vascular tissues. It is limited internally by the primary phloem and externally by the endodermis. Where the latter is lacking, the pericycle merges into the cortex. In width, the pericycle ranges from one to several rows of cells. In some roots its continuity may be interrupted where the protoxylem abuts on the endodermis; it is lacking only in certain very

small and structurally reduced aquatic roots, and perhaps also in similar stems. Where it seems to be lacking, as in most woody stems, its apparent absence is due to the absence of the endodermis, in which case the pericycle is confluent with and histologically similar to the cortex. When one or two rows of cells thick, it consists normally of parenchyma, but when thicker, it is usually sclerenchymatous, at least in part. Pericycle fibers are prominent features of many stems, both woody and herbaceous. In the early stages of development of woody stems and in herbs these fibers may contribute largely to the support of the stem. Pericyclic fibers are arranged in various ways: as continuous, uniform, or irregular bands (Fig. 52); as scattered, isolated strands; as clusters "capping" the primary phloem strands; as groups alternating with the protophloem groups. Such fibers are normally lignified, as are those of *Cannabis* (hemp), but may be of cellulose, as in *Linum* (flax). Economically important fibers, such as these, are frequently called bast fibers, but this term is best avoided in technical use (Chap. IV). Pericyclic fibers are often similar to fibers of the cortex and to those of the secondary phloem. All or any of these constitute commercial "bast."

In roots, the pericycle is narrower than in stems and is normally parenchymatous and more homogeneous (Fig. 104). This is the region of origin of the meristems which form lateral roots and often of the first phellogen layers, as well as of secondary cambium in anomalous steles. It is doubtless for this reason that the pericycle of roots was formerly known as the *pericambium*. Adventitious roots and stems also arise commonly in the pericycle. In old roots the cells of the pericycle may become sclerified or even suberized.

The parenchyma cells of the pericycle share with similar cells in other regions the function of storage. Secretory cells and canals, laticiferous cells, and other specialized cell types may occur in the pericycle.

THE ENDODERMIS

Limiting the stele on the outside is a cylindrical sheet of cells, one layer thick, without intercellular spaces, and with structural features unlike those of other cells. This layer is called the *endodermis*.

Structure of the Endodermis.—The cells constituting the endodermis are vertically elongate with end walls mostly transverse. In cross section they are of various shapes, but are usually more or less oval or elliptical with the longer axis in a tangential direction. The cells are living and possess fairly abundant protoplasm and large nuclei. Starch is frequently present; tannin and mucilage often occur; and sometimes, as in *Apios*, crystals are abundant. The features peculiar to the endodermis lie in the structure of the wall. This may be thick or thin, the latter condition being the more common; but its radial and end walls, or some part of them, are usually thickened and cutinized or suberized. In the thin-

walled cells the cutinized areas are in the form of strips which run completely around the cell on the inner surface of the radial and end walls (Fig. 50). These strips may be as wide as the entire radial wall or be

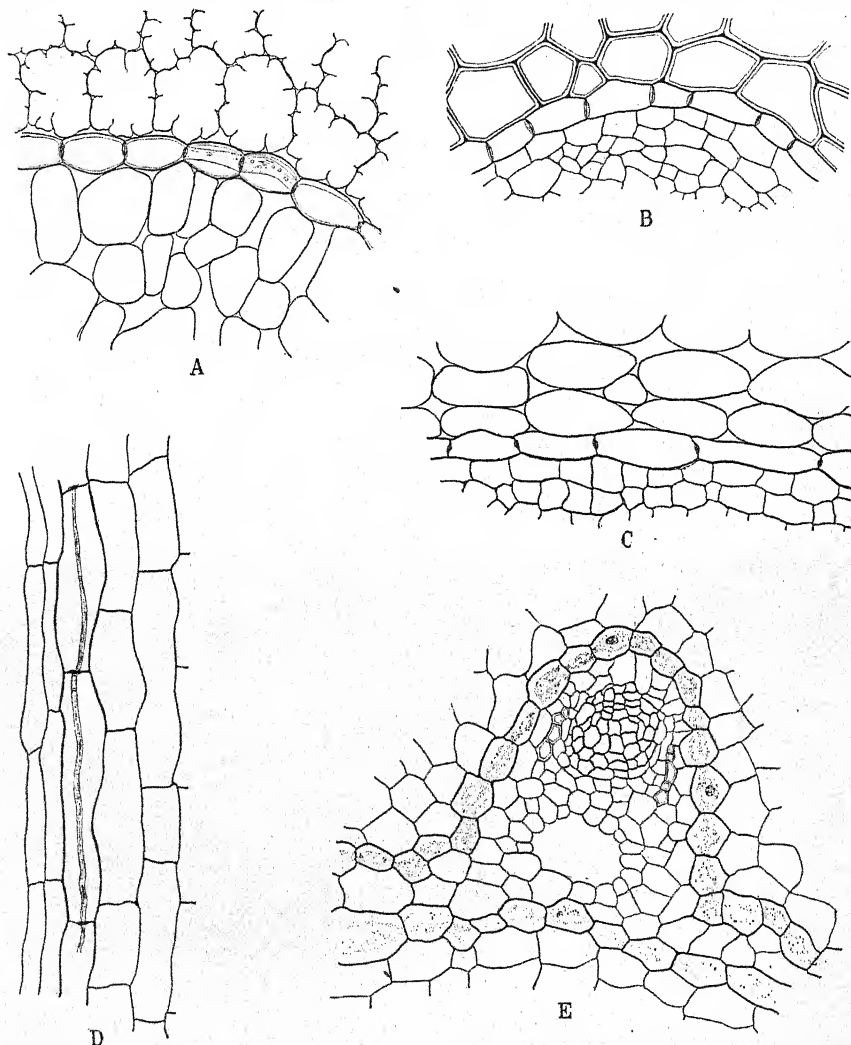


FIG. 50.—The endodermis. A, cross section in leaf of *Pinus*; the Casparian strips are seen in cross section, and in face view on the end walls. B, cross section in rhizome of *Polypodium*. C, D, cross and longitudinal sections in stem of *Lobelia*, showing the radial dots, and the Casparian strips in face view on the radial walls. E, cross section of outer and inner endodermis in stem of *Equisetum*; the protoplasts are plasmolized, but retain connection with the Casparian strips.

extremely narrow and thread-like. They may be merely areas in the wall, or may form marked thickened bands or ridges. Such areas or bands of additional wall thickening are known as *Casparian strips* (after Caspary

who first carefully studied them). In cross section the strips appear as dots (Fig. 50, A, B, C), and are often called *Casparian dots*, or *radial dots*. Where the strips are wide, abundant pits occur through them. The end walls are unpitted, or are lightly pitted, and the tangential walls are probably unpitted. Where the walls are thick, the entire wall, or only the radial and the inner tangential wall, is thickened (Fig. 51). The thickening is so great in many cases that the lumen becomes very small.

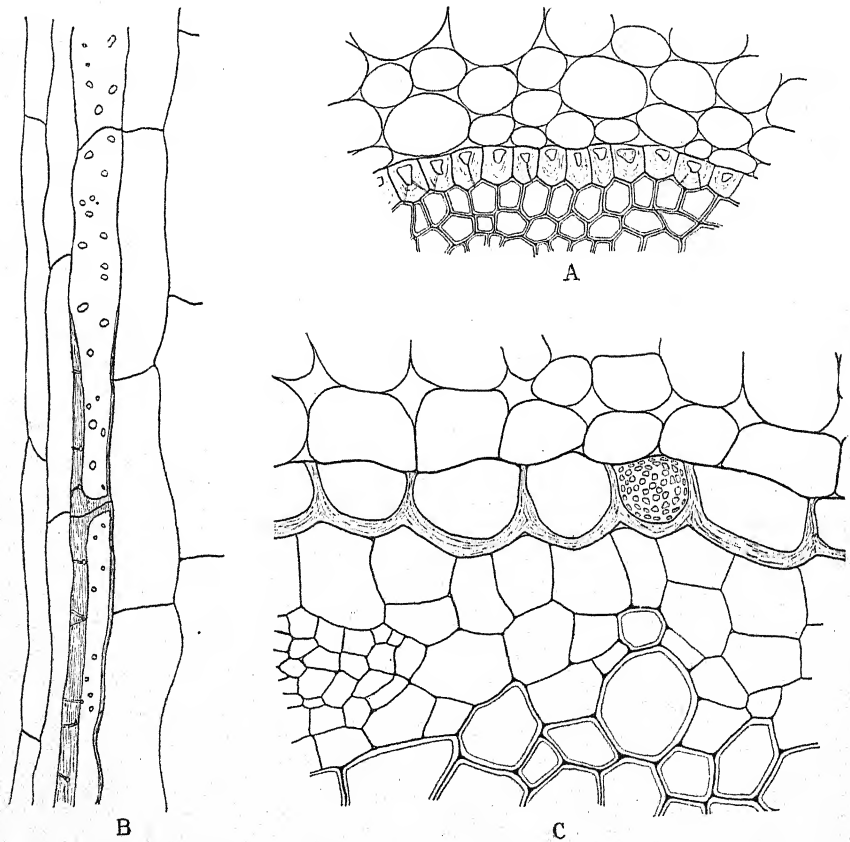


FIG. 51.—The endodermis; thick-walled types. A, B, cross and longitudinal sections from root of *Smilax rotundifolia*. C, cross section from root of *Musa sapientum*.

These thickened walls are suberized and cutinized and often to a considerable extent lignified. The thickened radial and inner tangential walls usually have numerous, small, simple pits. This type of endodermis (as well as other unusual types) has been called a *phloëoterma*, a term which has also been used as synonymous with endodermis. The word is now less commonly used. In a few plants the thick-walled endodermis has occasional, isolated, thin-walled cells which have no cutinized por-

tions. Such cells are known as *passage cells*, or *transfusion cells*. They are situated opposite the protoxylem cells.

Occurrence and Position of the Endodermis.—In its position in the plant body the endodermis is definitely a layer surrounding vascular tissue. Rarely, however, does it touch vascular elements, since the pericycle lies between. In roots the first protoxylem cells sometimes are in contact with the endodermis, but in stems the interruption of the pericycle is very rare. An endodermis may limit vascular tissue on the inside as well as on the outside, shutting it off from the pith. An endodermis thus internal to the vascular tissue is called an *inner endodermis* (Fig. 50, *E*). Such a layer is not structurally distinct from the outer endodermis, since the two may be continuous through leaf and branch gaps. The endodermis not only limits the vascular tissue of the axis, but may also surround the vascular bundles in leaves. It is not, however, a constant structural feature of vascular plants. It occurs throughout the roots of nearly all plants (Fig. 104), and largely throughout the plant body in the pteridophytes (Fig. 116, *B*). In gymnosperms it is characteristic of the leaves (Fig. 138, *A*), but is mostly absent in stems. In angiosperms it occurs in the stems of a considerable percentage of herbaceous forms, probably in the majority of cases. It also occurs in aquatic plants and species of moist habitats (Fig. 139, *A, B*); in creeping plants and in many seedlings; in rhizomes and some leaf bases; and in the bases of certain stems though it may be lacking in the upper parts. It is absent in woody stems and in the leaves of angiosperms generally. In herbaceous plants the endodermis occurs more commonly in the more highly specialized families, especially in the gamopetalous and apetalous dicotyledons and the monocotyledons.

Function of the Endodermis as Related to Structure.—The function of the endodermis has been a matter of much discussion since it was first studied, and is still largely in question. Many functions have been ascribed to it. These are based largely on its obvious relation to water and to vascular tissue. The endodermis appears to be a sort of watertight layer between xylem and surrounding tissues, especially where the organs in question are in a moist or wet situation. It occurs, however, also in many plants of dry soil, and in the leaves of xerophytic gymnosperms. Its absence in woody twigs may possibly be due to loss in evolution, since continued secondary growth destroys this layer. The endodermis further appears as a sort of water dam in that it always lacks intercellular spaces and the walls are more or less cutinized or suberized, so that in the thin-walled type, water may pass through the endodermis only through the tangential walls and through the protoplast, that is, through a semipermeable membrane. For this reason it has been looked upon as a diffusion layer separating regions of different osmotic pressure, and as a diffusion layer preventing loss of mineral nutrients, or

of food, from vascular tissue.³ It is believed by some students to be connected with root pressure, possibly controlling and maintaining this pressure.

In the thin-walled endodermal cells the behavior of the protoplast on plasmolysis, when the protoplast shrinks from the tangential walls but not from the radial walls (Fig. 50, *E*), suggests that water does not enter the cell from the radial walls. Such is not proof, of course, that water may not pass through the radial walls. In fact, much doubt has been cast, through recent studies of the chemical nature of the wall, upon the "water-tight" nature of the endodermis. The Casparian strips are of the nature of secondary wall layers laid upon a primary wall. The latter is often cellulose or "lignocellulose," and hence a thin strip of permeable wall may lie between the cutinized strips. Such a passageway is so slight, however, that the suberization may be said to cut down permeability to a large extent, and render the wall essentially impervious. Further, the strips are themselves in many cases definitely lignified and without evidence of cutin or suberin. Prominent Casparian strips appear in many cases to consist of a lignocellulose core with a coating of suberin. Still further, there are occasionally found definite endodermal layers without evidence of Casparian strips. Such layers may be vestigial in nature. Thus, it appears evident that the endodermis may be, at least to a slight extent, directly permeable by water.

Among the many and diverse functions which have been assigned to the endodermis at various times are the following. The endodermis was first believed to be a mechanical protective layer, a sort of inner, accessory epidermis. And, as such, the phloëoterma type in monocotyledonous roots may serve to some extent when the cortex has sloughed away, but the majority of endodermal layers are of delicate nature.

The general impermeability of the endodermis has suggested that this layer is an air dam, preventing the water-conducting cells from becoming clogged with air.

The persistence of starch in endodermal cells has suggested theories—now long abandoned—that the endodermis is a "starch sheath," a carbohydrate-conducting or storage layer, or a layer limiting storage to the inside or to the outside. The presence, type, and behavior of starch grains in the endodermis of certain plants have also led to the theory that this layer is an orienting "organ," the starch grains being statoliths which, by alteration of position in the cytoplasm, cause sensory stimuli leading to change in orientation of the organ. Such a function can be characteristic of the endodermis only of certain plants, and of parts of organs, since starch grains are not always found in endodermal cells, and in many types of such cells, owing to the presence of gum, crystals, etc., cannot "fall" from one position to another as the orientation of the organ is changed.

The function of the endodermis is thus in question. That it frequently has to do with the relations of water and xylem seems to be without doubt. It is probable that its specific functions in different plants vary greatly, since types of endodermis characterize families to some extent. Secondary functions doubtless also exist, and the primary function may have been lost in some instances.

Many of the facts regarding its occurrence in plant groups and regarding its variation suggest the possibility that the endodermis is an ancient structure of much physiological and perhaps morphological value, which has become modified in the course of phylogenetic development. In part, it may still retain its original relations and functions; in part, it may be more or less vestigial in nature; and in other cases it may have become specialized or modified in adaptation to new functions, as is frequently the case with vestigial structures. It has disappeared in woody twigs where continued secondary growth occurs.

Morphologically, the endodermis is commonly considered the innermost layer of the cortex. In this treatise it is looked upon as the outermost layer of the stele. It is, however, of little importance to assign the layer definitely either to the cortex or to the stele; it is a separating layer. It is here considered as belonging to the stele, since it must logically be so if the inner endodermis is a part of the stele. (The question of whether the pith is of stelar or cortical nature is outside the field of the present discussion.)

THE CORTEX

That portion of an axis which surrounds the central cylinder and is separated from the cylinder by the endodermis is the *cortex*. It is limited on the outside by the external uniseriate layer of the axis, the epidermis. In good usage the term "cortex" applies only to the definite region thus morphologically distinct, and only to the *primary* cells and tissues developed therein. Distinction is sometimes made between "primary cortex" and "secondary cortex"—the latter term being applied to secondary tissues developed within the primary cortex from cortical cells, chiefly to periderm. Such a use is, however, misleading, since all similar layers, such as those formed in the secondary phloem, are also loosely termed "secondary cortex." This usage is, of course, due to confusion resulting from the use of the term "cortex" in the loose sense of an outer part or covering, and in the physiological sense of any protective outer layer. The term "cortex" is best restricted to the definite primary region.

In thickness, the cortex varies from a few to a great many rows of cells (Fig. 52). (It is essentially parenchymatous in nature, but may contain many kinds of cells arranged in many ways. Collenchyma occurs only in the cortex, where it often constitutes a large proportion of the

tissues. Ridges, and in angular stems the corners, may consist entirely of this temporary supporting tissue. Fibers and stone cells occur freely as well as do secretory and storage cells of various types. Fibers more commonly occur in sheets or in large strands; they are often associated with the epidermis, forming below it an accessory outer protective layer, a hypodermis, or with the pericyclic fibers with which they may merge. The term "hypodermis" is applied to a layer of supporting or protecting cells of any type which lie immediately under the epidermis

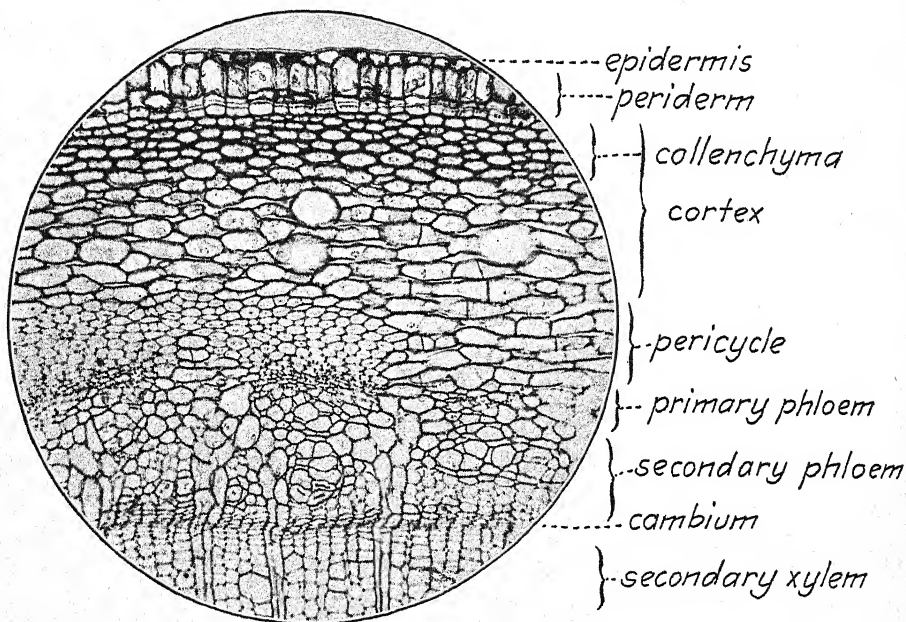


FIG. 52.—The cortex in a woody stem, *Magnolia acuminata*. The cortex consists of collenchyma and parenchyma. The cells of the latter are in tangential rows, due in part to continued radial division as an accommodation to diameter increase in the stem. Secretory cells are present. The thick band of fibers is pericyclic. Beneath this lie primary phloem groups, more or less crushed, and beneath these secondary phloem with fibers and sieve tubes. The cambium and secondary xylem are also shown. Below the epidermis a periderm layer is beginning to develop.

and reinforce this layer in some way. The cortical parenchyma cells normally contain chloroplasts, and definite specialized photosynthetic tissue may be formed (Fig. 137). The cells are arranged loosely or closely, and commonly no definite plan of arrangement occurs. Tangential rows may be conspicuous, and in specially modified roots and stems, such as those of aquatic plants, symmetrical radiating sheets of cells may occur. The cortex of roots is more homogeneous than that of stems and in the majority of cases consists of parenchyma only (Figs. 104, 110).

The various cell types in the cortex serve various functions, but it is evident that the cortex is primarily a protective layer. Such functions as support, photosynthesis, storage, etc. are secondary.

THE EPIDERMIS

The epidermis constitutes a layer over the entire outer surface of the plant body, continuous except for stomatal and lenticellular openings. In meristematic regions it is, of course, undifferentiated, and in older stems and roots it is destroyed by secondary growth. It is rarely of more than one layer of cells thick. The cells are living, with a large central vacuole and thin peripheral cytoplasm. Minute leucoplasts are often present, but chloroplasts are absent except in the guard cells of stomata and in plants of moist, shaded, or aquatic habitats. Mucilage, tannin, and crystals occur occasionally in the cells. The cells vary much in size and outline, but are essentially tabular. They are closely fitted together and are often lobed, toothed, or flanged in various ways, the projections dovetailing into those of other cells and strongly interlocking the cells (Figs. 54, 130). The cells of leaves, and especially those of petals, are more complex in this respect than are those of other organs. Epidermal cells often have unevenly thickened walls, the outer and the radial walls being much thicker than the inner wall (Figs. 135, *B*; 136, *D*). This additional thickness and the cutinization of the walls is of much importance from the standpoint of mechanical protection and of prevention of loss of water. The cuticle (Chap. II) adds greatly to the efficiency of the epidermis in the latter respect.

Ontogeny and Duration of the Epidermis.—In ontogeny, the epidermis, or dermatogen, is early set off from the subjacent meristematic cells. Later increase in the cells of the epidermis is brought about wholly by anticlinal division; the uniseriate condition is thus early established, and is maintained during the life of the epidermis. Where the epidermis persists for some time, and the stem slowly increases in diameter, as in herbs and some woody plants, continued slow division may go on in the epidermis, which thus is accommodated to the increased surface. Changes in epidermal cells, other than those involved in the development of phellogen layers, are rare. In roots, the epidermal cells, and also those of the outer cortex, generally become lifeless, and lignified or suberized after the root hairs cease to function. In perennial stems epidermal cells live until the development of a periderm layer cuts off their water and food supply. In leaves, flowers, and most fruits they normally live as long as does the organ of which they are a part.

Function of the Epidermis.—In function, the epidermis is chiefly a covering layer which provides against harm from loss of water and against mechanical injury. It also may serve minor functions, such as photosynthesis and secretion. Parts of the epidermis may be structurally modified to serve some important physiological function, as, for example, the secretory tissue of nectaries, the stomata of leaves and stems, and the absorbing hairs of roots.

Root Hairs.—In roots, many or all of the epidermal cells become *root hairs*. In the ontogeny of such cells the outer wall expands, forming a long, tube-like process, in shape and structure a typical hair (Fig. 53). The walls of epidermal cells in general, and especially those of the projecting hairs, are thin and delicate. They are commonly of cellulose and permit ready diffusion of water and dissolved substances. It is by absorption through root hairs that the chief supply of water and mineral nutrients is obtained. These structures are ephemeral, persisting usually but a few days or weeks, after which they collapse and the remains of the cells and of adjacent cells become suberized or lignified. Root hairs with thick lignified walls are reported in certain Compositae where they are said to persist into the second growing season.

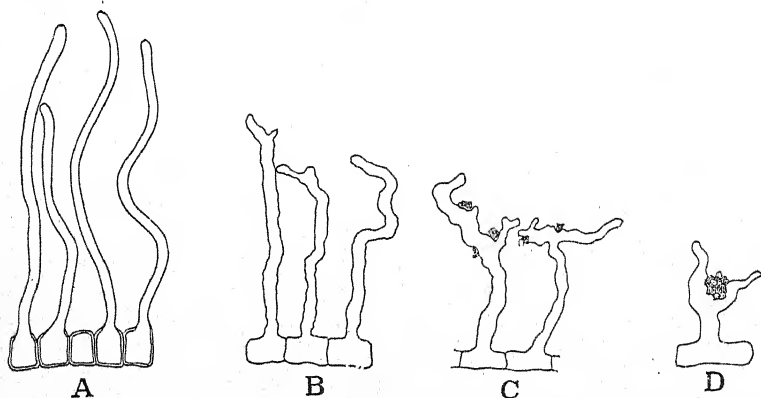


FIG. 53.—Root hairs. A, grown in water or moist air. B, grown in moist soil. C, D, grown in dry soil. (Particles of soil adhere in C and D.) (After Schwarz.)

The Stoma.—The openings in the epidermis through which gaseous interchange takes place between the intercellular spaces of the subepidermal cells and the atmosphere are known as *stomata* (singular, *stoma*). These openings are spaces between two specialized epidermal cells which are known as *guard cells*, since changes in size and shape of these cells determine the opening and closing of the stoma (Fig. 54). Ordinarily, these two cells alone of the epidermal cells adjacent to the stoma differ from epidermal cells. Where other cells also are modified because of the presence of the stoma, and contribute in some way to the functional activity of the guard cells, such cells are known as *accessory cells*. This type of cell is restricted almost wholly to xerophytic plants (Chap. XIV). The term “stoma” is also, and perhaps preferably, applied to the opening in the epidermis plus the surrounding guard and accessory cells. In this usage the orifice is known as the *stomatal opening*, or *stomatal aperture*. The term *stomate* is also in good usage as a synonym for the term “stoma” in both the senses in which the word is used.

Structure and Action of the Guard Cells.—In all stomata the opening and closing is dependent upon changes in the turgor of the guard cells, increased turgor causing the stoma to open. The way in which the guard cells operate varies in different species according to the shape of the guard cells and the thickening of parts of the wall. In one common type the

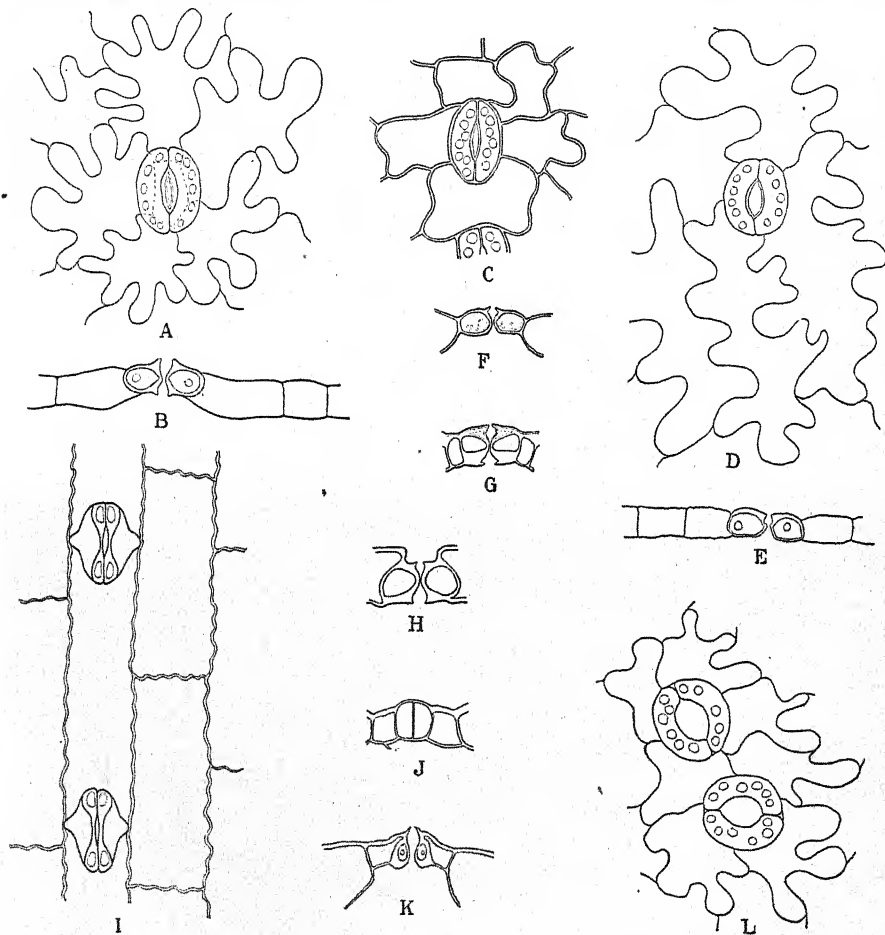


FIG. 54.—Stomata. A, B, from *Solanum tuberosum*, in face view and cross section. C, from *Pyrus Malus*. D, E, from *Lactuca sativa*. F, from *Medeola virginica*. G, from *Aplectrum hymnale*. H, from *Polygonatum bistlorum*. I, J, K, from *Zea Mays*: I, face view; J, cross section through end of stoma; K, median cross section. L, from *Cucumis sativus*. (F, G, H, and J, after Copeland.)

walls of the guard cells are uniformly thickened and the guard cells are elliptical as seen in transverse section (Fig. 54, F). With an increase in turgor these cells tend to become round in cross section, thus separating the closing walls of the stoma. In other types opening in a similar manner, the wall is unevenly thickened (Fig. 54, E). A modification of

this same principle of change in the shape of a cell which is asymmetrical in cross section is found also in other types of stomata in which the walls are unevenly thickened. In these types the cell wall may be very thick, except at two points or regions known as "hinges." The lumen of such cells is elliptical or oval as seen in cross section, and with an increase of turgor tends to become round, thus causing a stretching or flattening of the thin parts of the wall with consequent opening of the stoma (Fig. 54, *B, G*, the hinges being the median point on the side of the aperture and the entire opposite wall). In another common type the walls of the guard cells next the aperture are somewhat thicker than those on the opposite side of the guard cell (Fig. 54, *H*). Increase in turgor in guard cells of this type causes the thinner walls to stretch, and this, in turn, causes the entire guard cell to become more sharply curved; and since the concave side is next the aperture, the opening is enlarged. In the grasses and some other plants the ends of the guard cells are thin-walled and enlarged, whereas the central parts next the aperture are thick-walled and rigid (Fig. 54, *I, J, K*). With increase in turgor these bulbous ends of the guard cells become distended and press against each other, thus forcing the rigid centers to separate and the stoma to open. In all cases decrease in the turgor of the guard cells results in the closure of the stoma.

The above statements are descriptive only of general stomatal structure. Other more or less distinct types exist, the variations being largely those of shape of guard cells and of position of the thickened areas of their walls. The details of structure about the opening vary greatly with different species, but are sometimes constant for large groups, as, for example, the grasses, and the gymnosperms. Difference in habitat may cause great differences even within a genus, the most extreme modifications being found in xerophytes (Chap. XIV). The essential structural features are the same for all stomata, however.

The guard cells differ from other cells of the epidermis of which they are a part in that their protoplasts are more richly cytoplasmic, with a prominent nucleus, and chloroplasts and starch grains are usually present.

Functionally, stomata are of the very greatest importance, since it is through these openings that gaseous interchange between the intercellular space systems and the outer air takes place. And upon this diffusion through the stomates largely depend the functions of respiration, transpiration, and photosynthesis. The physiological processes and the physical laws involved in the activity of stomata do not fall within the scope of this treatment.

Occurrence of Stomata.—Stomata occur on leaves and stems, their abundance being perhaps correlated somewhat with the amount of photosynthetic activity of the underlying tissue. Normally stomata are

much less numerous on stems than on leaves, but under conditions where the leaves are reduced, they are abundant on the stem where photosynthesis is an important function of the cortex. The stomata of floral parts and of aquatic plants are often abortive or lacking.

Hairs.—Appendages of the axis or leaves which consist only of epidermal cells are known as *hairs*, or *trichomes*. Such appendages are uni-

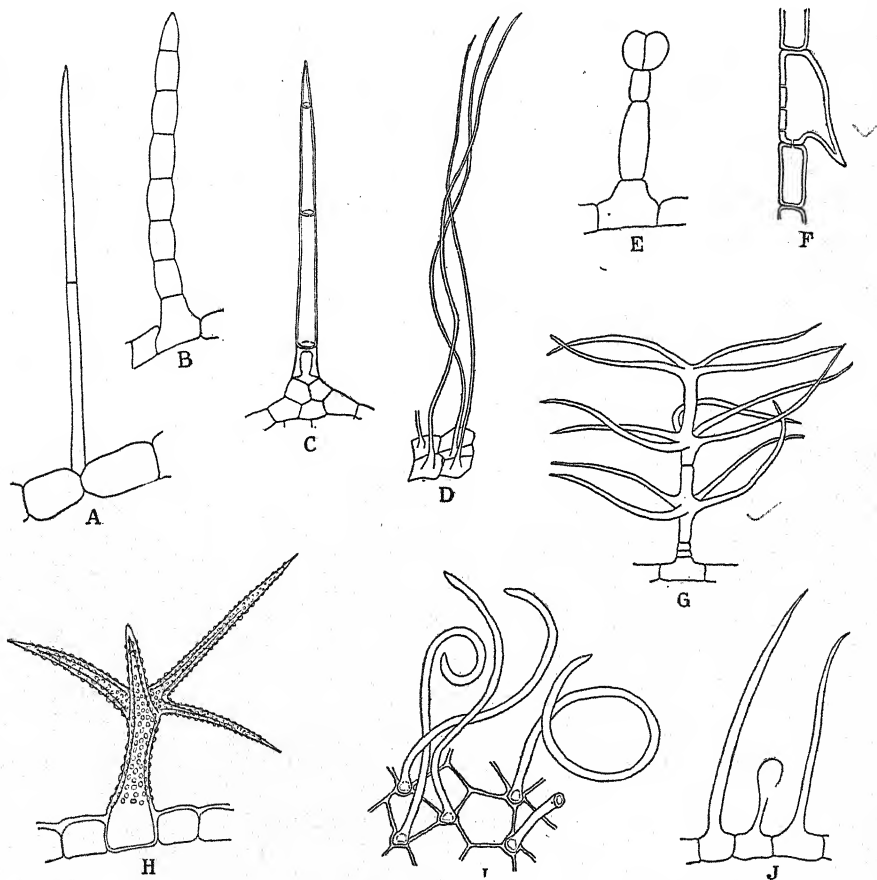


FIG. 55.—Hairs. A, from corolla of *Epigaea*. B, from leaf of *Coreopsis*. C, from leaf of *Cucumis*. D, from stem of *Onopordum*. E, from corolla of *Phryma*. F, from leaf of *Arena*. G, from young leaf of *Platanus*. H, from stem of *Aubrietia*. I, from fruit of *Rubus strigosus*. J, from calyx of *Heliotropium*.

cellular or multicellular and occur in very many forms (Fig. 55). All transitional stages occur between the typical epidermal cell and one in which the outer wall is prolonged into a tube sufficiently pronounced to be considered a hair. Such intermediate cells, called *papillose cells*, are common upon petals (Fig. 129, C) and many leaves. So-called unicellular hairs may be formed merely by the prolongation of the outer wall of the

epidermal mother cell, as in root hairs (Fig. 53); or the basal portion, lying within the epidermis proper, may be cut off from the projecting portion. Unicellular hairs assume numerous shapes, including elaborately forked and branched types. Multicellular hairs likewise are found in innumerable types, and range from simple linear hairs of a few cells to complex, intricately branched, or massive structures, involving considerable areas of the epidermis. Stinging hairs (Fig. 41, *A*), scales, and many glandular hairs (Fig. 41, *B*, *C*, *E*) are complex multicellular structures.

The cells of hairs may be dead or living. If alive, the protoplasts contain little cytoplasm, unless the hair is associated with secretion of some type when the cytoplasm is abundant and richly granular. The thickness of the wall and its chemical nature vary greatly. Such hairs as those on the fruit of the peach and raspberry (Fig. 55, *I*), the flower of the willows, and the bud of the grape are very thick-walled. Cutinized, lignified, and cellulose hairs are frequent. Cotton "fibers" are cellulose hairs. Other hairs, such as those of kapok (*Ceiba*), are of some economic value.

Hairs are concerned with many functions, major and minor. It is, however, in the reduction of transpiration through the additional coating they provide that they are probably most important. Root hairs are morphologically typical hairs.

THE PRIMARY VASCULAR SKELETON

The primary vascular tissues of a plant form a definite vascular skeleton, which may, in a way, be compared with the skeleton of an animal. In the various organs and parts of plants, the vascular tissues differ in arrangement, position, method of attachment, etc. from those of other organs or parts of organs, and these differences are constant and characteristic. The skeleton of a species has a definite and fixed plan and differs more or less from that of other species. The skeletons of the different larger groups of plants—as of the larger groups of animals—differ from one another in important respects; the skeletons of smaller groups differ in less important respects, but may be very varied in structure. Great diversity of vascular structure thus exists among plants, and all conditions from very simple to highly complex are found.

The Stele.—Owing to the fact that the axis is cylindrical or columnar, the skeleton of this part of the plant body as a whole is naturally more or less of the same type. The vascular tissues of the stele in their simplest condition form a solid, rod-like column in which the phloem surrounds the xylem. A stele with its vascular tissues arranged in this way is known as a *protostele* (Figs. 56, *A*; 103). The protostele is not only a very simple kind of stele, but also is clearly the primitive type from which all others have been derived in the course of evolutionary speciali-

zation. The vascular column of a protostele when seen in cross section may be circular; symmetrically angular, such as triangular; stellate, with long-projecting arms; or irregularly rounded and variously lobed. A kind of stele differing from the protostele chiefly in that a pith is present in the center is the *siphonostele*, or *solenostele* (Figs. 56, B; 112, A, E). This type of stele has been derived from the protostele and represents a stage in evolutionary advance. Like the protostele, the siphonostele shows various outlines in cross section, but is commonly rounded. Two types of siphonostele are found: *ectophloic*, where phloem occurs only on the outside of the xylem; and *amphiphloic*, where phloem occurs on the inside of the xylem as well as on the outside. When the siphonostele is broken up into a network or a series of longitudinal strands, it

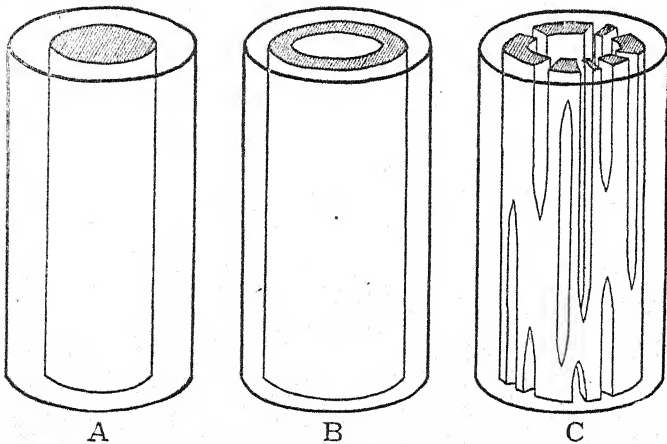


FIG. 56.—Diagrams illustrating the types of arrangement of vascular tissues in steles. A, protostele. B, siphonostele. C, dictyostele.

becomes a *dissected siphonostele*, or *dictyostele* (Figs. 56, C; 112, B, F). In some cases, as in the majority of monocotyledons, the vascular bundles of the dictyostele—sometimes known as *meristeles*—are scattered through the pith and cortex so that the semblance of a stele or ring is lost. Such a condition has clearly developed in evolution from the siphonostele or dictyostele, and is considered to belong to this type.

The term *monostele*, which has sometimes been used as synonymous with protostele, was applied originally to those steles in which the vascular tissues form a unit structure. In contrast with the monostele was the “polystele,” a type of stele in which the vascular tissues are in the form of strands, each one of which resembles more or less the entire vascular cylinder of protostelic plants. Thus, the protostele and the unbroken siphonostele have frequently been called monosteles, and some types of dissected siphonosteles termed “polysteles.” The bundles of a dissected siphonostele—especially when the stele is amphiphloic and the

bundles amphicribal—resemble in cross section small protosteles, and the stele therefore appears like a multiple protostele; hence the term “polystele” was given to such a central cylinder. It is now understood, however, that this type of stele is merely a broken-up siphonostele, and that polysteles, as multiple steles, probably do not exist. Hence the term “monostele” has little use, and is commonly replaced by the more specific protostele and siphonostele, the broken siphonostele being called a dictyostele. The term “polystele,” as applied to any type of dissected siphonostele, suggests inaccurate morphology, and therefore should not be so used.

Two theories exist as to the method by which, in evolutionary change, the siphonostele has been derived from the protostele. According to the “expansion theory,” the central portion of the stele does not become vascular, but remains less specialized, becoming pith. The pith is, therefore, according to this theory, morphologically vascular tissue. The term “expansion” is unfortunate here, since expansion of the protostele has not necessarily occurred. According to the “invasion theory,” the cortex has invaded the central cylinder in the course of the phylogenetic development of vascular plants, leaf and branch gaps being the openings through which the change has occurred. Under these conditions the pith is obviously not stelar in nature. A discussion of these theories lies outside the scope of this book. It seems, however, to have been established beyond much question that, in seed plants at least, the pith is morphologically extrastelar in nature. In most of the pteridophytes the same condition obtains; in a few the pith is possibly stelar in nature.

Occurrence of Stelar Types.—The protostele, being the primitive type, is found more commonly among the primitive plants. It occurs in many of the ancient fossil forms, and in the present-day flora is characteristic of the club mosses and a few of the ferns. It occurs in the roots of nearly all plants. The siphonostele or some modification thereof is found in all other living plants. The ectophloic siphonostele is characteristic of the stems of gymnosperms and of angiosperms generally, and is without question the most common type. The amphiphloic siphonostele is typical of ferns and of some families in the angiosperms. The dissected siphonostele occurs in many ferns and in the angiosperms to some extent, especially in the herbaceous types. However, in the two groups of plants the situation is not altogether the same, morphologically.

Leaf Traces.—Prolongations of the stelar vascular supply extend into leaves (Fig. 57, A). Such vascular bundles constitute the *leaf traces*, or *foliar traces*. The bundles supplying a single leaf range in number from one to many, but the number is largely constant for a given species and often for families and even for larger groups. The term “leaf trace” is used in two somewhat different ways—as applied to any bundle which extends to a leaf, and to the complex of bundles which supplies a given

leaf. Thus it may be said, for example, that three leaf traces are characteristic of a given plant, or that the leaf trace of the plant in question

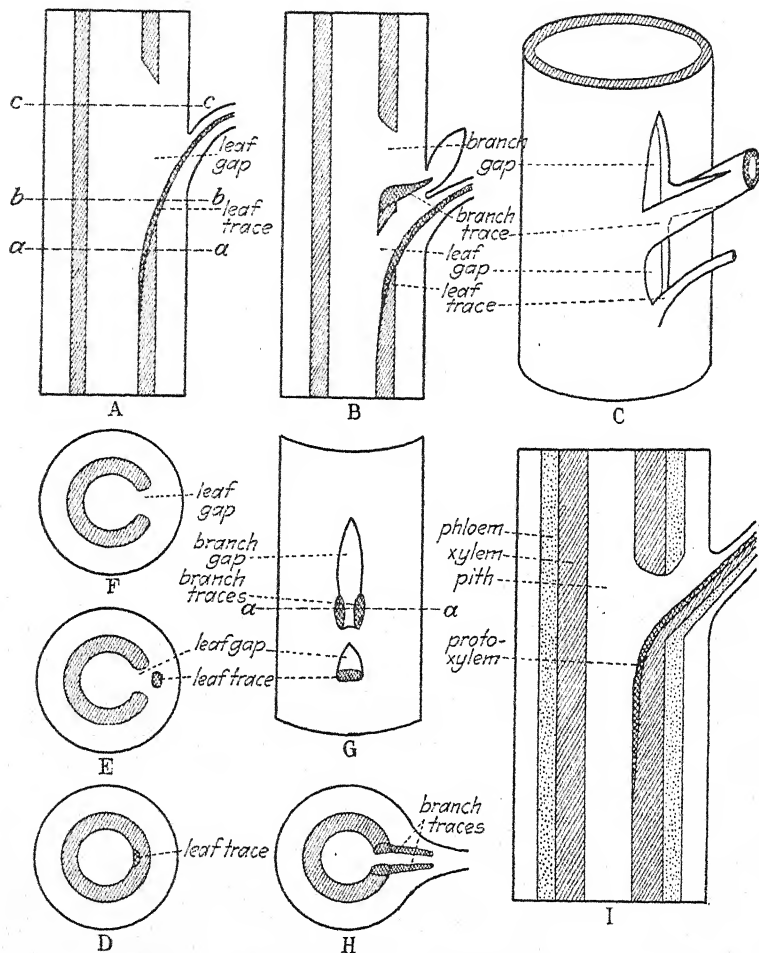


FIG. 57.—Diagrams illustrating leaf and branch traces and gaps. A, longitudinal section of node through leaf trace and gap. B, similar to A, but with branch trace and gap also present. C, view of vascular cylinder showing departure of leaf and branch traces, and the gaps associated with each. D, E, F, cross sections through stem illustrated in A at levels a-a, b-b, and c-c, respectively. G, face view of outside of cylinder shown in C, the leaf and branch traces cut away at the surface of the cylinder. H, transverse section of G at a-a. (In diagrams A-H the vascular tissue is not differentiated as xylem and phloem; the traces are doubly cross-hatched. In I, more detailed structure is shown, protoxylem, metaxylem, and phloem being indicated.)

consists of three bundles. The term *leaf supply* is sometimes used to indicate the sum total of the traces passing to one leaf.

Structurally, leaf traces are strands of primary vascular tissue, the proximal portion of which (that lying inside of the phloem) consists of

xylem alone. In all cases the xylem of a trace is, in part, protoxylem. The distal parts of the trace contain phloem, and secondary xylem and phloem may be added. Since the trace is merely an extension of the vascular system of the stem—either as a definite, abruptly separated branch of that system, or as a strand gradually set off as a distinct part—there is not usually a definite point of origin of a trace. The trace as an identifiable, protoxylem-containing strand may, indeed, often be followed down the stem for some distance below the level at which it begins to swing outward, and there found to merge with other traces or with the xylem of the primary cylinder. Distally, the limit of a leaf trace is usually understood to be the base of the petiole. The bundles within the petiole or leaf base are not usually called traces.

The length of a leaf trace depends upon the course followed through the cortex: if this is directly radial and nearly horizontal, it is short (Fig. 59, *M*); if obliquely upward, it may be long (Fig. 59, *O, P*), especially if the stem is partly encircled at the same time (Fig. 59, *I, J*). The term "trace" is applied to these bundles from the point in the stele where they first become evident as foliar supply bundles to the base of the leaf. The number of leaf traces characteristic of a species or of a larger group is the number of bundles which leaves the stele to enter any one leaf. These in their course through the cortex may fork or fuse in various ways. Such changes are even more common in the petiole where complex structural conditions often arise. Further fusion and ramification occur in the leaf blade according to the type of leaf and of venation characteristic of the plant in question. The vascular supply to stipules is derived from the lateral traces, usually within the cortex.

Branch Traces.—The primary vascular supply to lateral branches is also derived from the stele of the main axis in the form of two bundles, or, less often, one bundle. These strands are termed *branch traces*, or *ramular traces* (Fig. 57, *B, C*). Branch traces, like leaf traces, are connected with the first-formed parts of the primary stelar skeleton. Thus, all parts of the axis and the appendages are tied together by the primary vascular system. Where the branch supply consists of two traces, these bundles unite within a short distance, forming a complete stele (Fig. 57, *C*); where but one trace occurs, this strand has usually the cross-sectional form of a crescent or horseshoe with the opening downward, and the cylindrical stele of the branch is formed by the closure of the opening as the trace passes out.¹

¹ It should be borne in mind that terms of motion are used here—and elsewhere in the book—in the description of the course of bundles, merely for the sake of ease in expression. For example, a leaf trace does not "pass out of," "run through," or "enter" a region in the sense of actual movement (or even necessarily in the sense of increase in length in the stated direction, though this may be the method of devel-

Leaf and Branch Gaps.—In the majority of vascular plants the outward passage of a leaf or branch trace is associated with the formation of a break or interruption in the vascular cylinder around and above the point of departure of the trace (Fig. 57). This opening, through which the cortex and pith become continuous, is known as a *gap*—a *leaf gap* in the case of a leaf trace, and a *branch gap* in the case of a branch trace. Leaf gaps are constant in appearance in the great group of vascular plants known as the Pteropsida. This group is made up of the ferns, the gymnosperms, and the angiosperms. Leaf gaps do not occur in the Lycopsidea, a group which includes the clubmosses, horsetails, and a few other similar plants. Branch gaps are present in all vascular plants which possess a pith. In protosteles, gaps, of course, do not occur, since no pith is present. Gaps are not associated with root traces.

Leaf gaps vary much in width and in longitudinal extent. Their size is not directly related to the size, type, or persistence of the leaf. Commonly, in the gymnosperms and angiosperms, leaf gaps are small, extending but a short distance above the point where the trace leaves the vascular cylinder. In the ferns, leaf gaps are generally larger and may extend for considerable distances, even through several internodes. Branch gaps are commonly larger than leaf gaps and extend for greater distances in the axis.

The Breaking of the Vascular Cylinder by Gaps.—The vascular cylinder is broken up in different degrees by the presence of leaf gaps. Where the gaps are small and of limited longitudinal extent, the cylinder is but slightly broken by them (Fig. 58, *G*); but where they are large and elongate, extending through one or more internodes, the common condition in the ferns, the siphonostele is dissected, becoming a dictyostele (Fig. 58, *H*). The degree to which a siphonostele is dissected depends upon the extent of the gaps and upon the closeness of the nodes. Where the gaps overlap, due to their great length or to the shortness of the internodes, the cylinder consists of a network of bundles which in cross section appear as a circle of discrete strands (Fig. 58, *H*, *I*). By the presence of leaf gaps alone the cylinder may thus be broken into distinctly separated strands. Branch gaps still further complicate the

opment); nor does a "gap" or a "break" occur in a vascular cylinder as an actual opening up of the tissues. In the construction of a building the position of the gap which later becomes a window is determined, and the opening is formed, in early stages of framework development; the window is not cut through a completed wall. The structural plan of a region in a plant body is developed gradually out of the meristem which is building up that part of the plant. Stele traces, gaps, etc. are present from early stages, in the position and of the type characteristic of the mature region in question. For example, procambial cells develop early in the position in which the leaf trace will lie when mature; and procambium is lacking in the area in which a gap later becomes evident.

structure. The primary vascular cylinder may thus be complex in the arrangement of its vascular tissues, especially in nodal regions where the outgoing leaf and branch traces are also present.

Branch traces are separated abruptly and depart as soon as freed from the cylinder (Fig. 57, *B, C*); leaf traces, on the other hand, may be freed from the cylinder and yet maintain their position in the circle for some

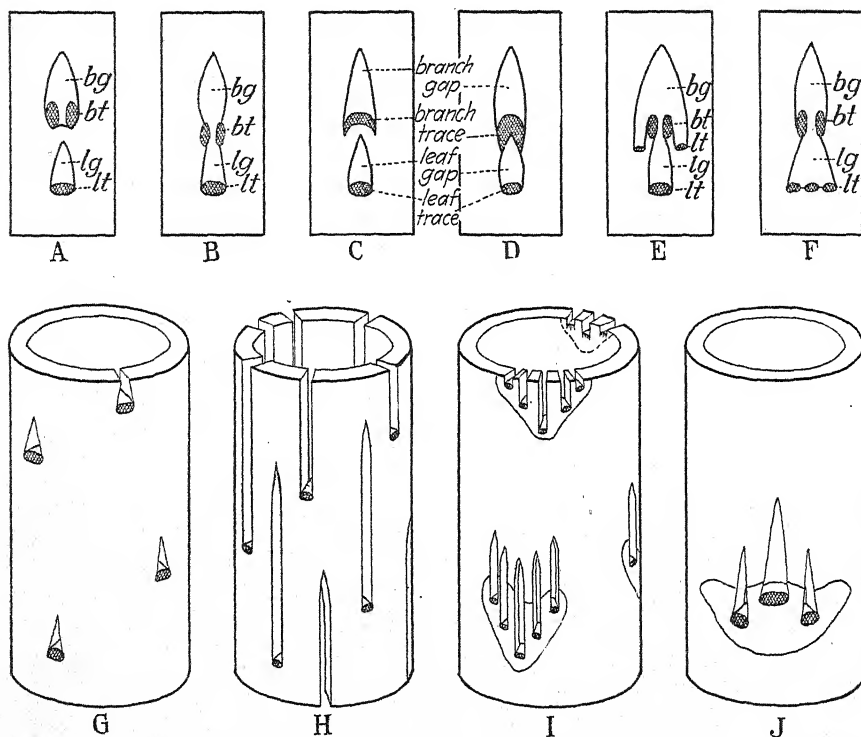


FIG. 58.—Diagrams showing variety of form of leaf and branch traces and gaps. A-F, face views of nodal region, showing traces cut away at outside of vascular cylinder and the gaps: A-D, one leaf trace, E, three traces and three gaps, F, three traces, departing together, leaving one gap; A, the leaf gap closed below the two branch traces and the branch gap; B, the leaf gap fused with the branch gap; C, the leaf gap closed below the departure of the single branch trace; D, the single branch trace departing at the top of the leaf gap; E, three leaf gaps from as many traces, all fused with the branch gap; F, one leaf gap from three traces, fused with the branch gap. G-J, diagrams of vascular cylinders showing various amounts and types of dissection by leaf gaps.

distance before passing out into the cortex (Fig. 59, *A, D*). Below the point where the trace is separated from the cylinder it is in many cases evident for some distance as a distinct, though not isolated, strand, chiefly of protoxylem (Fig. 59, *A, E*). This distinctness of the strand in the xylem cylinder is due to the type and size of cells composing it, these being different from those of the adjacent xylem. Externally, the trace

is not definitely limited, merging into the xylem of the cylinder (Fig. 59, *E*). Such a downward extension of the trace may be very short or lacking, or may be several internodes in length.

A leaf-trace bundle is commonly freed from the stellar cylinder on both sides simultaneously, but one side may remain attached for a time, even while the trace swings out into the cortex (Fig. 59, *F*, *G*, *H*). The trace then appears to depart from the side of the gap rather than from

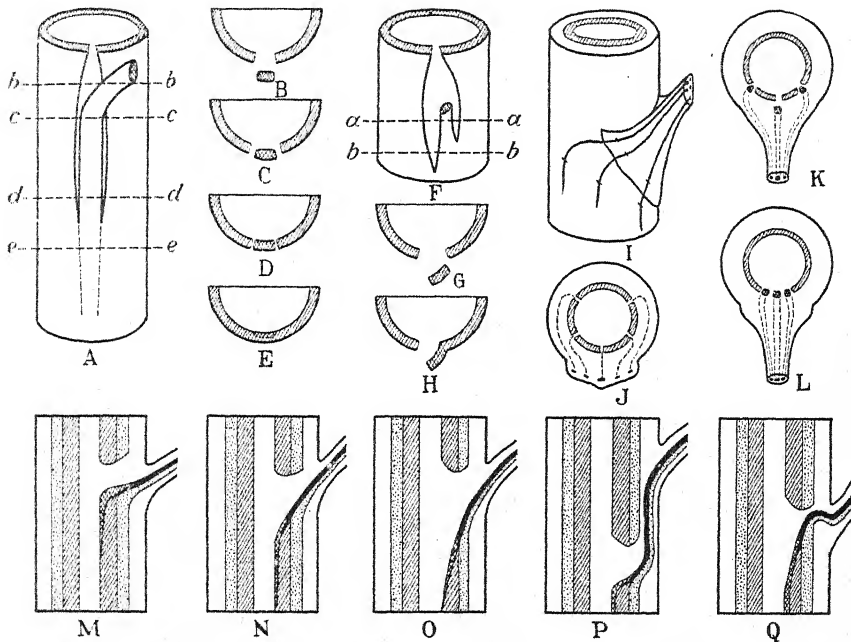


FIG. 59.—Diagrams showing variations in the method of departure of leaf traces. *A-F*, the trace freed some distance below its departure from the cylinder; *A*, face view; *B-E*, cross sections at levels *b-b* to *e-e*, respectively. *F-H*, the trace freed on one side before the other; *F*, face view; *G* and *H*, cross sections at levels *a-a* and *b-b*, respectively. *I* and *J*, traces departing from the cylinder in regions not underlying the leaf attachment—"girdling traces": *I*, course of traces seen from the outside, the points of departure from the cylinder and of entrance to the petiole indicated; *J*, the course of the traces projected from their points of departure to the petiole. *K*, projected course of three traces arising separately. *L*, projected course of three traces arising from one gap. *M-Q*, longitudinal sections of nodes showing various courses of the departing trace.

its base. Where a trace departs from the side of a gap or other opening in the cylinder already present, the gap theoretically associated with the new trace is not evident, being merged with the larger gap.

The Number of Leaf Traces in the Plant Groups.—The number of traces supplying the leaf ranges, as above stated, from one to many. In the pteridophytes there is in most cases one, though sometimes there are two or many; in gymnosperms, one or two; and in angiosperms,

one, three, five, or many. Three is perhaps the primitive number for the last group; where there is one this is either the result of fusion of the original three in evolutionary development, or of reduction of the three to one by the loss of the lateral bundles. Three and one are the most common leaf-trace numbers in the flowering plants, three being characteristic of nearly all the Amentiferae, and of such families as the Rosaceae, Aceraceae, and Compositae; and one of the Lauraceae, Ericaceae, and Labiatae. The number of traces is almost wholly independent of the size, type, and duration of the leaf, and of the nature of its attachment. Many plants with large leaves, such as *Fraxinus*, have one trace; others, such as *Juglans*, three; and still others, such as *Aralia*, many; plants with small leaves likewise have one, few, or many traces. The floral bracts of *Salix*, which are minute, ephemeral leaves, have three traces. Leaves with clasping bases may have many, as in the Umbelliferae, or one, as in the Caryophyllaceae.

The Departure of the Leaf Trace from the Vascular Cylinder.—The traces of a leaf normally depart individually, often at considerable distances from one another laterally about the stem, as well as vertically on the axis (Fig. 58, *G*; 59, *K*). In many cases, however, the traces depart side by side (Fig. 58, *F*; 59, *L*). Only one gap is then formed by the group. Traces most frequently depart from that segment of the stele which lies directly beneath the attachment of the leaf. Where there is more than one trace, the median trace appears opposite the center of the leaf, the laterals arising successively higher and higher in the stem and farther and farther around the cylinder from the median trace (Fig. 59, *I*, *J*). Traces may depart even from the side of the stele opposite to that on which the leaf stands. Such traces enter the base of the petiole directly if the latter clasps the stem extensively, or may "girdle" the twig in the cortex, swinging around the stem as they pass upward through the cortex to the petiole base. When traces thus pass around the stem for some distance in their course from vascular cylinder to petiole, they have been called "girdling traces" (Fig. 59, *I*, *J*). The leaf traces of the cycads are girdling traces of an extreme type. Of the bundles of a leaf supply the median trace is commonly the largest; the laterals form a series progressively smaller toward the margins of the leaf base. Lateral traces may, however, be stronger than the median trace, as in the potato plant (Fig. 62).

The angle at which the trace leaves the central cylinder varies greatly, being usually very small, the strand departing gradually from the pith and passing obliquely, sometimes almost vertically, through the cortex (Fig. 59, *N*, *O*, *P*). Less commonly, the trace passes outward nearly at right angles to the stele (Fig. 59, *M*), entering the leaf base after a very short course through the cortex. Branch traces also commonly pass out nearly at right angles.

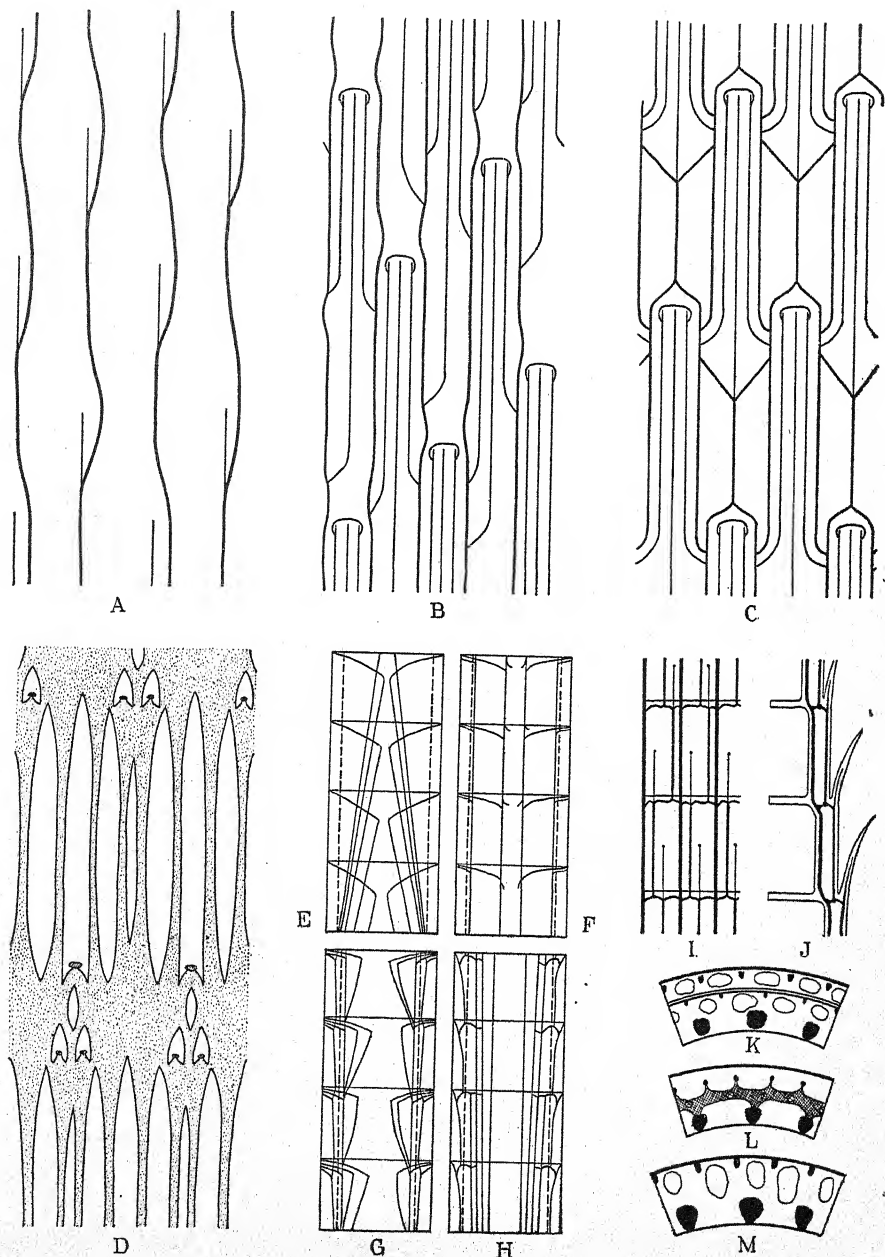


FIG. 60.—Diagrams of the primary vascular system (or of a part of the system) of stems. A–D, the cylinder split open and shown in one plane: A, *Thuja occidentalis* (the lines represent broad bands, separated by narrow breaks); B, *Chenopodium glaucum*; C, *Iresine paniculata*; D, *Ephedra distachya*. E–H, types of bundle course in the monocots—the horizontal lines indicate nodes, the dotted vertical lines imaginary cortical limits: E, a palm type; F, *Tradescantia virginica*; G, rhizome of *Acorus Calamus*; H, *Scirpus cyperinus*. I–M, *Dulichium arundinaceum*; I, bundle system seen in one plane; J, longitudinal section; K–M, cross sections; K, above the node; L, through the node; M, below the node. (B, C, after

The Dissection of the Vascular Cylinder by Reduction.—To repeat, the primary vascular cylinder may be broken into isolated strands by gaps alone. However, in many plants, both herbaceous and woody, a more extensive reduction and dissection has occurred, in which the primary cylinder has in evolutionary development not only become thin radially, but also broken into discrete strands, separated by bands of non-vascular tissue. This is the condition in herbaceous plants of a certain type where the non-vascular strips are wide, such as *Ranunculus*, *Impatiens*, and *Pilea*; in some vines, both woody and herbaceous, such as *Clematis*, *Apios*, and *Menispermum*; and in some trees and shrubs, such as *Platanus*, *Lonicera*, and *Berberis*, where the non-vascular bands are narrow.

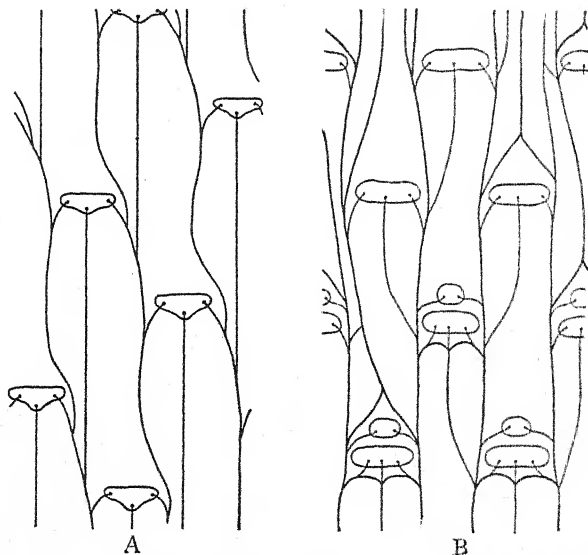


FIG. 61.—Diagrams of primary vascular systems. *A*, *Populus canadensis* ("Carolina poplar"); only the larger bundles shown. *B*, *Impatiens pallida*, the complete system: the lower nodes show branch traces; the system becomes more complex in successive internodes, a new bundle being added at each node. (The internodes are much shortened in these diagrams.)

The primary vascular cylinder of these plants is a network of anastomosing bundles, the strands forming a definite pattern which is constant for the species in question. The structure of this network varies greatly (Figs. 60, 61, 62), and depends in part upon the number of traces to the leaf and upon the phyllotaxy. Anastomosis takes place usually close to the nodes and long, straight bundles may then extend from nodal region to nodal region. In the majority of monocotyledons, and in some dicotyledons, the bundles do not lie in a cylinder, but are arranged somewhat in the form of a loose sheaf, so that they appear in cross section as scattered bundles. In some ferns, such as *Pteris*, and in a considerable

number of dicotyledons, for example, *Dianthera*, the bundles constitute an open cylinder, but a few of the strands run through the cortex or the pith. In both the monocotyledons and in these forms of anomalous structure, a definite system of arrangement exists.

Cauline and Common Bundles.—Where the primary cylinder is thus made up of independent strands, two types of bundles are recognized: *cauline bundles*, those which are definitely bundles leading through the stem and which have no direct relation to leaves (Fig. 62, the large bundles); and *common bundles*, those which pass through the stem for a greater or less distance but which terminate as leaf traces (Fig. 62, the small bundles). Cauline bundles in most cases are connected laterally with common bundles and with leaf traces, and certain portions of the vascular system often cannot be distinguished as definitely cauline or common. The stem bundles of some species are wholly common bundles, perhaps the usual condition in dicotyledons and gymnosperms; those of others, cauline and common bundles in various proportions.

General Structure of the Primary Vascular Cylinder.—In the majority of angiosperms, both herbaceous and woody, the primary vascular cylinder of the stem is not so extensively broken up by interfascicular parenchymatous bands as in the forms just discussed. It is perforated only by comparatively small and more or less remote leaf and branch gaps. In such cylindrical sheets of tissue, there are in most plants more or less prom-

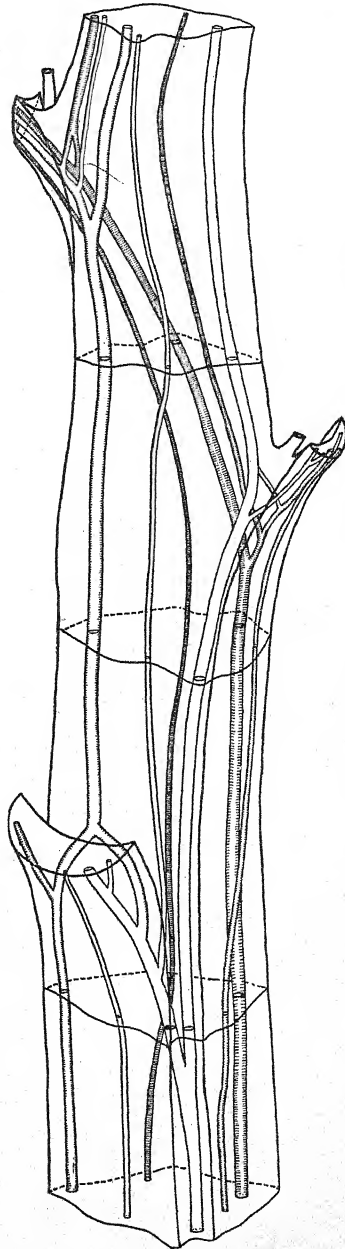


FIG. 62.—The primary vascular system of the stem of *Solanum tuberosum*. The complex nodal structure is repeated at each node, so that, except for the position of the bundles in the stem, all nodes and all internodes are alike. The large bundles are cauline bundles; the small ones, common bundles. (After Artzschwager.)

inent ridges projecting into the pith (Fig. 63, *G*, *I*). These ridges correspond morphologically with the common and cauline bundles of the more dissected stele. In this case however, there are no bundles, as such, since the ridges are all bound together by the thinner areas of primary vascular tissue which lie between. In the ontogeny of the vascular cylinder these ridges mature first, the larger and most deeply project-

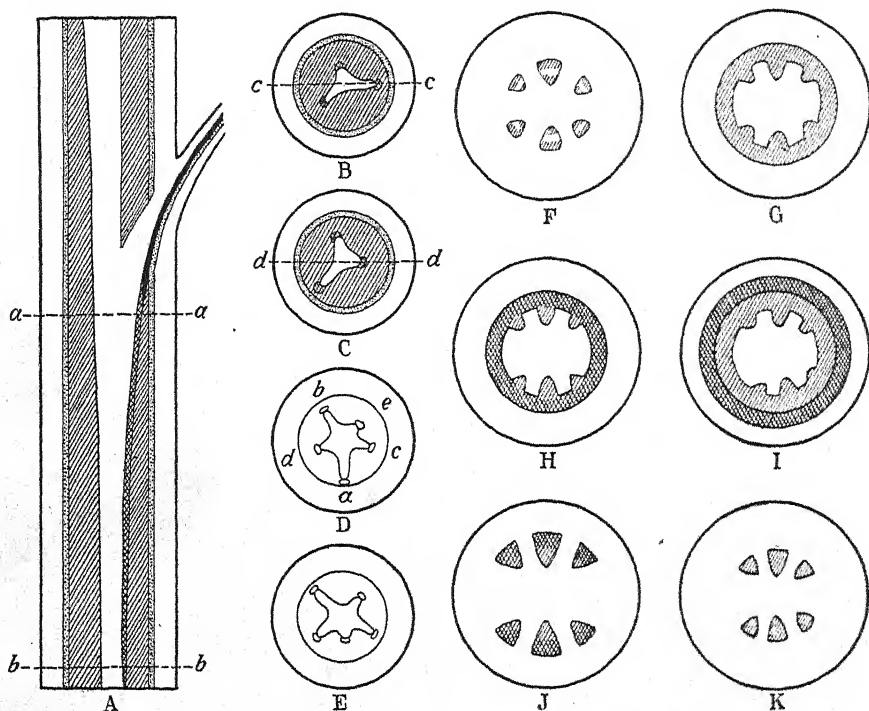


FIG. 63.—*A-E*, diagrams showing the effect upon pith form of the gradual departure of the trace: *A*, longitudinal section (in plane *c-c* of *B*); *B* and *C*, cross sections of stem shown in *A* at levels *a-a* and *b-b*, respectively (the traces depart according to one-third phyllotaxy); *D*, *E*, cross sections of a similar stem with two-fifths phyllotaxy, *D* being one internode higher than *E*; the traces are labeled, in order of their departure, *a*, *b*, *c*, *d*, *e*. *F-K*, cross section diagrams showing the form of the primary vascular cylinder, the inwardly projecting ridges being common and cauline bundles and leaf traces; *F*, young stem in which only the first primary xylem, forming the ridges, is mature; *G*, the ridges connected by later formed primary xylem; *H*, the ridges connected only by secondary xylem; *I*, like *G*, but with secondary xylem also; *J*, the first-formed primary bundles not later connected, and secondary xylem formed on the outside of the bundles; *K*, like *J*, but without secondary xylem. (Phloem is not shown in *F-K*.)

ing ones earliest. The innermost parts of these early formed strands consist of protoxylem. Later, less prominent ridges develop, and these, together with the still later formed connecting strips of primary xylem, are wholly metaxylem. When the stem is very young and the connecting flanges of tissue are still undifferentiated from meristem, the ridges con-

stitute discrete bundles (Fig. 63, *F*). When the primary vascular tissue has all matured, uniting the bundles into a cylinder (Fig. 63, *G*), these first-formed strands are still prominent, owing to their position nearer the center of the pith; because of this prominence, they have often been considered, erroneously, to constitute the entire primary vascular system. In those plants where during primary growth the early formed bundles are not later connected laterally by primary vascular tissue—a cylinder of isolated primary strands resulting—the bundles may be united by secondary tissues (Fig. 63, *H*). A complete cylinder may thus be formed—embracing or embedding the first-formed primary bundles—either by primary or by secondary growth (Chap. VI). In many cases it is difficult to determine whether the connecting strips are primary or secondary. Both primary and secondary tissues are commonly developed in both herbaceous and woody forms (Fig. 63, *I*). Where these connecting bands, either primary or secondary, do not develop, a stele of the so-called “herbaceous type,” with isolated strands, is formed (Fig. 63, *J, K*). This condition is thus structurally comparable with the early stage of a complete vascular cylinder when only the first-formed bundles have appeared.

As seen in a cross section of the mature primary cylinder of a stem, the most prominent of the ridges projecting into the pith are in many cases common bundles. These bundles may be, however, the downward extensions of the leaf traces which pass out at the next node above. In such cases they become, as the node is approached less, and less pronounced as wedges projecting into the pith. Sooner or later they swing outward, either gradually (Fig. 63, *A*) or abruptly, and come to lie in indentations of the vascular cylinder rather than on projecting points (Fig. 63, *B-E*). Ridges of the pith then project into the vascular cylinder. As the traces pass farther and farther out, the pith ridges increase in extent and the vascular cylinder is broken by the presence of the leaf gap thus formed. The shape of the pith as seen in cross section may clearly indicate the phyllotaxy of the plant in question. Thus a one-third phyllotaxy may be evident in a three-lobed pith, as in *Alnus* (Fig. 63, *A, B, C*); a two-fifths in a five-lobed pith, as in *Quercus* and *Populus* (Fig. 63, *D, E*); a one-half by an oval or elliptical pith, as in *Ulmus*. In long internodes the projecting ridges of the pith are prominent only where the traces gradually pass obliquely outward; the more gradual the departure of the trace the longer and often the deeper the lobe. Where the number of traces per leaf is more than one, the lobing may be obscured, but lateral traces commonly are smaller and pass out much more abruptly than do median traces, so that the characteristic lobing is still evident. “The number of first-formed strands, whether ultimately still free or fused into a cylinder, may be few or many. These become more or less obscure where an unbroken cylinder is formed, whether this be of primary nature alone or

whether secondary growth is also concerned in the completion of the cylinder. In monocotyledons the large number of bundles and the complexity of the system often render the scheme of arrangement difficult of interpretation.

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(See also References for Chap. III)

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CHAPTER VI

THE ORIGIN AND DEVELOPMENT OF THE SECONDARY BODY AND ITS RELATION TO THE PRIMARY BODY. THE CAMBIUM

That the primary plant body is in itself structurally and functionally complete is evident from the fact that in many forms it alone constitutes the plant, for example, the majority of monocotyledons and the pteridophytes. In the gymnosperms and in most dicotyledons, however, primary growth is soon followed by secondary growth, which usually becomes, both structurally and functionally, the more important. Secondary growth is effected by definite layers of initials—in vascular tissues, by the cambium; in other tissues, by similar meristems. These growing layers provide additional and constantly renewed conducting, supporting, and protecting tissues. Primary growth chiefly increases the length of the axis and adds the appendages; secondary growth increases the diameter of the axis (after the initial increase), and is responsible in most cases for the greater part of the mature plant body, supplying the requisite support, protection, and conduction for the large body of woody plants. Only in some of the monocotyledons, for example, a few of the palms, is a large body present which is wholly primary in nature. The majority of the larger monocotyledons, including many of the palms, the woody yuccas, and other lilies, possess secondary growth of a special type (p. 159).

Secondary tissues fall into two groups: the vascular tissues, those formed by the true cambium; and those, such as cork, formed by other similar but secondary meristems.

The Origin of the Cambium from Procambium.—As explained in the preceding chapter, the primary vascular skeleton is built up by the maturing of the cells of the procambium strands or cylinder to form xylem and phloem. In plants which have no secondary growth, all cells of the procambium strands mature to form vascular tissue, and further increase in the amount of this tissue is impossible, except by unusual methods. On the other hand, in plants in which secondary growth later appears, a part of the procambium strand remains meristematic and gives rise to the cambium proper. The cambium, then, commonly represents a persistent portion of the apical meristem (Fig. 42), a section which remains meristematic and which becomes transformed into a growing layer of a different type.

Since the maturation of procambial cells usually proceeds progressively toward the center of the procambium strand the cells in the cen-

tral region are the last to become permanent. Where cambium develops, these last central cells do not transform into permanent xylem or phloem cells, but retain their meristematic activity indefinitely as cambium cells. In the early stages of cambium development there is a more or less irregular zone of meristematic tissue between the areas of primary xylem and phloem. At this time the protoxylem elements are usually mature and the metaxylem cells are in the process of maturation. The beginnings of cambial activity and the development of the last of the primary metaxylem therefore occur simultaneously.

As commonly understood, the true cambium does not exist as such until there is established a definite tangential row of initials which divide regularly in the tangential plane. Just before the formation of such a sheet of tissue there is a transitional period during which cell division is taking place in various planes in the central procambial zone, but tending in the later stages of development to occur more and more in the tangential plane only. As these tangentially dividing cells mature, those retaining their meristematic activity become arranged in a definite tangential row, becoming the true cambium, which then forms secondary tissues. It is thus evident that it is impossible to distinguish sharply between primary and secondary vascular tissues, since the two merge into one another, both in position and in development. Further confusion is also caused by the fact that in many cases, as, for example, in *Lobelia* and *Trifolium* (Figs. 46, B; 117, A), the primary xylem elements are arranged in radial rows. These rows do not always, however, lie in the same radii with rows of cells formed by the true cambium, and the transitional zone between primary and secondary xylem is usually without regular cell arrangement.

In roots, the formation of the cambium differs from that in stems because of the radial arrangement of the alternating xylem and phloem strands (Chap. X). Here the cambium arises as discrete strips of tissue in the procambial strands inside the groups of primary phloem (Fig. 106). Later, by lateral extension through parenchymatous tissues the strips of cambium are joined in the pericycle opposite the rays of primary xylem. In this extension the parenchymatous cells become actively meristematic and by division form a cambium much as in the formation of some types of interfascicular cambium from the procambium in stems (p. 131). Because of the place of origin of the cambium in roots, this meristem does not, in its early stage of development, form a symmetrical cylindrical structure, but rather, as seen in cross section of the axis, an irregular band of tissue which curves outward around the ends of the xylem rays and inward inside the strands of phloem. Commonly, however, secondary tissue formation is most rapid next to the groups of phloem, so that the cambium as seen in the transverse section of older roots forms a circle. In some cases development of secondary tissue by the cambium

inside the phloem groups goes on to a considerable extent before lateral extension around the xylem is complete, so that a cambium ring is present as soon as the segments join.

Fascicular and Interfascicular Cambium.—The first procambium to develop from promeristem is usually in the form of more or less isolated strands. In many plants these first-formed strands very soon become connected laterally by similar procambium strands between them or by the lateral extension of the first-formed ones, with the result that a

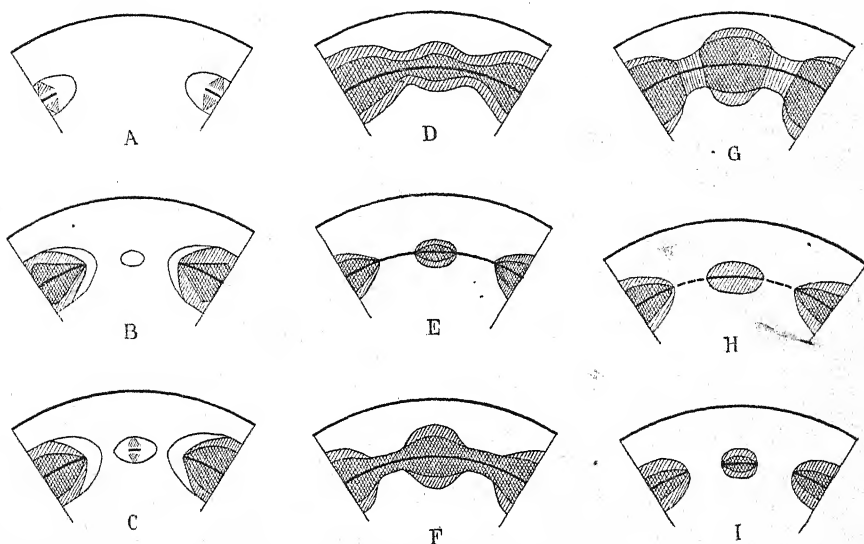


FIG. 64.—Diagrams to show the formation of the cambium cylinder in stems. (The primary vascular tissue is singly cross-hatched, the secondary, doubly.) A-D, successive stages in type where complete primary cylinder is formed: A, the first primary tissues are mature in the procambium strands and the cambium has appeared in the center of the bundle; B, C, the bundles have increased in size, secondary tissues are formed, and new small bundles are arising between the first; D, complete primary, secondary, and cambial cylinders are formed by the union of the bundles. E-F, type with complete cambium cylinder, but incomplete primary cylinder: E, the fascicular cambium has built up secondary tissues in the bundles; the interfascicular cambium has just arisen; F, secondary tissues complete the vascular cylinder. (The interfascicular cambium in E may arise in either of two ways—see text.) G, similar to E-F, but the interfascicular cambium forming only parenchyma. H, similar to E, but with a vestigial interfascicular cambium, which forms few or no vascular cells. I, primary cylinder of discrete strands, each with cambium and secondary tissues; no union by secondary growth.

practically continuous cylinder of procambium is formed. In the course of development this gives rise to a continuous cylinder of primary xylem and phloem and also of cambium. Ultimately, a cylinder of secondary vascular tissue will also be formed, arising in strands as does the primary cylinder (Fig. 64, A-D). In many species, however, especially in herbaceous forms, such as *Ranunculus* and *Impatiens*, the procambium strands, and hence the primary vascular tissues, do not fuse laterally but remain in discrete strands. In such cases the cambium likewise is in the form of

longitudinal bands, since it does not extend laterally beyond the limits of the primary xylem and phloem between which it arises (Fig. 64, *I*). Such strips of cambium then constitute the entire cambial meristem, as in *Ranunculus*; but, more often in herbaceous stems the cambium extends laterally from the first-formed bands across the intervening spaces until a complete cylinder is formed (Fig. 64, *E*). Where such extension occurs, the cambium may arise from thin sheets of procambium which become cambium in entirety, that is, without the previous formation of xylem and phloem by the procambial bands. In most such cases, however, the connecting, late-appearing sheets of cambium arise from parenchyma cells which have become permanent, or nearly so. The development of strips of cambium from permanent cells in this way makes these parts meristem of secondary nature, like cork cambium (Chap. IX). Thus in plants of this type a cylinder of cambium may be entirely primary meristem or may consist of alternate strips of primary and secondary meristem.¹ In either case, however, the tissues formed by this meristem are secondary throughout. To the strips of cambium which arise within collateral bundles the term *fascicular cambium* is applied, and the portions in the intervals between the bundles are known as *interfascicular cambium* (Fig. 117, *A*). The latter term is sometimes restricted to those strips of cambium lying between primary bundles which do not in their activity form xylem and phloem, but merely parenchyma, as in *Clematis*.

Between the condition found in the woody plants, where a complete cambium cylinder is formed from a complete procambium cylinder, and that condition frequent in herbs, where the cambium, even in the mature plant, is in the form of discrete strips, all intergrading conditions are found relative to the formation and activity of the interfascicular cambium. In herbaceous plants with woody cylinders the interfascicular cambium may be identical with the fascicular cambium in origin and function, but merely delayed in development from the normal procambium, which in those regions may form little or no primary vascular tissue. Such cambium forms normal secondary vascular tissues in the same way as the fascicular cambium, although in many cases the amounts formed are not so great (Fig. 64, *F*). The same structure may form from interfascicular cambium developed from more or less permanent parenchymatous tissues; but more frequently no real vascular tissue is formed, the cambium giving rise to parenchyma only, as in *Clematis*. In such cases, discrete collateral vascular bundles occur, which are separated by secondary parenchyma. This is apparently a specialized

¹ Since a continuous sheet of cambium is thus in some cases partly primary and partly secondary, it is apparent that the classification of meristems as primary and secondary is artificial; and that from a morphological as well as from a physiological viewpoint such classification has but little value. However, the classification is one of convenience in the study of meristematic development.

condition, found for the most part in woody vines and in some herbaceous forms. It has undoubtedly been derived in phylogeny from the woody condition and is not, as is frequently stated, a stage in the development of a woody cylinder by the fusion of vascular bundles. In some herbaceous stems, as in species of *Geum* and *Agrimonia*, for example, an incomplete, vestigial interfascicular cambium is found; its scattered cells divide but once or twice (Fig. 64, H).

The Time of Cambium Development in Stems.—In the stems of plants with well-developed secondary growth the cambium begins to differentiate from the procambium in a given region even before that region has ceased to elongate. The cambial derivatives do not, of course, mature as such at this time, but some divisions may take place, so that as soon as elongation ceases there may be simultaneous maturation of cambial derivatives and of primary metaxylem, although a considerable proportion of the latter usually mature first. As before stated, there is, therefore, a zone of maturing cells in which the primary and secondary tissues cannot be differentiated. Thus, in the majority of plants the formation of cambium is going on in the new parts of axes during the entire growing season or as long as the axes are increasing in length. In plants which have both intercalary meristems and secondary growth, as in some of the mints, cambium may be in an early stage of development in regions other than those near the tips of the axis. In general, it can be said that in plants which have secondary growth, stem elongation, whenever it may occur, is either accompanied by or immediately followed by cambium development. In some of the reduced herbs, which have very little secondary growth, cambial activity may be delayed for some time.

The Time of Cambium Development in Roots.—In roots, cambial development frequently does not take place so quickly after elongation ceases as in the stems of the same plant. In fact, in many of the smaller feeding roots, a cambium may not be formed at all, even though secondary growth occurs abundantly in the stems and larger roots. This condition is apparently an adaptation to the function of the root as an absorbing organ, since wherever extensive secondary growth arises the root is no longer capable of absorption in that region because of the destruction of the root hairs, endodermis, and cortex, and because of the usual immediate formation of periderm. Thus roots of some herbaceous plants may be without secondary thickening even though such growth occurs in the stems; and in some woody species a considerable proportion of fibrous rootlets contain only primary growth. In the main root system of both woody and herbaceous plants, however, the cambium arises soon after elongation has ceased.

Extent of the Cambium.—In the normal woody plant and also in many herbs the cambium forms a layer over the entire inner part of the

body, except at the growing tips of the axis where the cambium has not as yet been differentiated. The cambium of a part of a stem or root thus forms a hollow cylinder, and that of the entire plant a branching tubular structure. The whole layer is frequently spoken of as the *cambium cylinder*. Strand-like extensions of the cambium often occur in leaf traces, and at leaf and branch gaps above such traces there are breaks in the continuity of the cambium while the axis is young. Usually within a few weeks after the initiation of cambial growth, however—or at most within a few months, the length of time depending upon the size of the gap and upon other factors—the cambium extends over the gaps, gradually closing them from the edges. The extensions of the cambium in leaf and branch gaps are secondary in nature, appearing as new areas of meristem developing in the gap parenchyma by the division of certain parenchyma cells. Thus, in plants of this type the perforations of the cambial cylinder are closed, and the cylinder is henceforth unbroken except for the occurrence of wound areas.

In plants in which the stele is dissected, as in many herbaceous forms, the extent of the cambium is, as already stated (p. 132), no greater than the width of the collateral bundles of which the stele is comprised. In these cases the cambium consists of a broken cylinder of strips or bands of tissue. These bands follow various courses, according to the plan of the primary vascular system (Chap. V). The width of these strips or plates of cambium necessarily varies as greatly as does the width of the vascular bundles of which they are a part. In some reduced herbaceous forms the width of the strips is only a small fraction of the circumference of the stele.

Cambium is also found in the peduncles and pedicels, commonly in the petiole and larger vascular bundles of leaves, and rarely in the bases of monocotyledonous leaves.

Duration of the Cambium.—The extent of the functional life of the cambium varies greatly in different species and also in different parts of the same plant. In a perennial woody plant the cambium of the main axis lives from the time of its formation until the death of the plant. It is only by the continued activity of the cambium in producing new xylem and phloem that such plants can maintain their existence, since the functioning life of a given portion of these tissues is comparatively short. Cambium of this sort is never used up in the sense that all its cells mature to form vascular tissue. In leaves, inflorescences, and other deciduous parts, however, the functional life of the cambium is of short duration, in leaves possibly for a few days only in some cases, and in peduncles at the most for a few weeks. In these cases the cambium does not die but all cells mature to form vascular tissue, so that a layer of initials ceases to exist. Under such conditions the secondary xylem abuts directly upon the secondary phloem in the vascular bundle. In the annual stems of

pereunial plants and in the stems of herbaceous annuals generally, the cambium is also of this latter type, in that it is functionally active for a short time only and all cells mature into vascular tissues. In some of the specialized dicotyledonous herbs which have small, isolated vascular bundles or very thin vascular cylinders, very little secondary growth takes place. Some such forms lack secondary growth altogether or show so little that it is difficult to determine whether or not a true cambium is ever formed, since the last-formed metaxylem cells may be arranged in even, more or less radial rows simulating secondary xylem.

Effect of Cambial Activity upon the Primary Body.—Since the cambium arises between the primary xylem and primary phloem, a part of the primary body is enclosed by the newly formed tissues. This inner part, the pith and primary xylem, is completely shut off from the outer parts. It persists within the cloak of secondary tissues unchanged except for the ultimate disappearance of cell contents, and for certain chemical changes accompanying the death of pith and wood parenchyma cells. The pith is not crushed by secondary growth except in a few plants of anomalous structure, such as *Aristolochia*; nor is the primary xylem skeleton distorted as the stem becomes older. In many herbs the pith is destroyed by elongation of the axis and by the rapid expansion of the tissues outside the pith as the pith is maturing or shortly thereafter (Chap. IV). This, however, is not the result of secondary growth, and, in fact, usually takes place before secondary growth begins. The entire original primary body lying within the position first occupied by the cambium is to be found in the oldest stems and roots, structurally perfect as in the axis before secondary growth began. Thus the vascular skeleton, pith, gaps, and inner parts of leaf traces of the seedling tree are still present in the base of the old tree trunk.

The primary tissues lying outside the cambium—the primary phloem, the pericycle, the endodermis, the cortex, and the epidermis—are, on the other hand, pushed outward by the development of secondary tissues. Since the increase in circumference to which these tissues must be accommodated quickly surpasses the extent to which plasticity, or the slow primary growth which may still be going on, enables accommodation, these tissues are commonly either ruptured or crushed. The primary phloem in most plants is quickly affected, its cells being flattened and crushed. It may thus appear as a disorganized band of crushed tissue as seen in transverse sections of young stems and roots. Often it disappears early, the crushed cells being absorbed so that no traces of the tissue remain. The endodermis likewise is ruptured and lost soon after secondary growth begins. The pericycle and cortex, owing to their somewhat firmer structure, and frequently also to their partial accommodation by slow primary growth to the diameter increase caused by secondary growth, persist in many cases for a longer time. In most

plants with well-developed perennial secondary growth, however, these outer parts are sooner or later crushed, or broken open and killed by exposure to drying and by other types of injury; and especially by the shutting off of food and water supplies by cork layers which develop within them (Chap. IX). The dead parts are soon sloughed off by decay or by abscission, and, after a variable interval, ranging from a few weeks to several or many years in different species, the outer primary body disappears. Thus, secondary growth preserves intact the inner section of the primary body, but is responsible for the complete destruction of the outer portion. Exceptions to the loss of the entire outer part of the primary body occur in a few woody plants where the cortex persists for many years through the capacity of its parenchyma for slow primary growth. Such slow and long-continued growth of primary tissues obtains in the epidermis of some woody twigs; in the cortex and pericycle of the same and of similar plants; and in a few plants more or less throughout the stem, as in the trunks of some palms which lack secondary growth.

Outer primary tissues persisting unchanged after marked secondary growth has taken place are, of course, most conspicuous in herbaceous plants. In these forms the overlapping, in time of formation and in position in the axis, of primary and secondary growth is probably greater than in woody forms. Thus the outer tissues become accommodated to the increase in diameter due to secondary growth with a lesser degree of distortion than in typical woody plants. Often, however, as the stem becomes old, though the epidermis is not ruptured, the softer cells of the cortex, pericycle, and phloem become much compressed radially, as in *Aster*, *Linum*, *Cannabis*, and many similar herbs with thick, woody cylinders.

The Relation of Secondary Growth to Leaf Traces.—At nodes the projection of leaf traces makes the stem structure complex. With the increase in thickness of secondary xylem the bases of the leaf traces (those parts within the cambium cylinder) are buried; and since the cambium lies always between the xylem and the phloem (Fig. 65, *A*), the formation of new xylem causes the outward movement of all phloem as well as of the cambium itself, not only on the axis, but also on the trace (Fig. 65, *B*). Thus because of the place of origin of the cambium, secondary growth buries the proximal parts of the leaf traces; the innermost part, lying in the primary xylem, is without phloem and is buried without change; from the adjacent part the phloem is stripped away and pushed outward, and only the xylem of the trace is embedded in the secondary xylem of the stem (Figs. 65, 66). The length of the buried part depends largely upon the angle at which the trace departs.

Only short pieces of the trace lying outside the original position of the cambium are buried, however, since continued secondary growth, in forcing outward the cortex and phloem, in which the outer parts lie

embedded, breaks the trace in two, the distal part of the strand being torn away and carried outward with the tissues in which it lies. Rupture is due to the outward thrust of secondary growth laterally upon the trace (Fig. 67, A, B, C, D). However, this rupture does not occur until sometime after the leaf has fallen, commonly the first or second growing season thereafter. The secondary xylem of the first year embeds the inner part of the trace without injuring it, the phloem being pushed outward but not

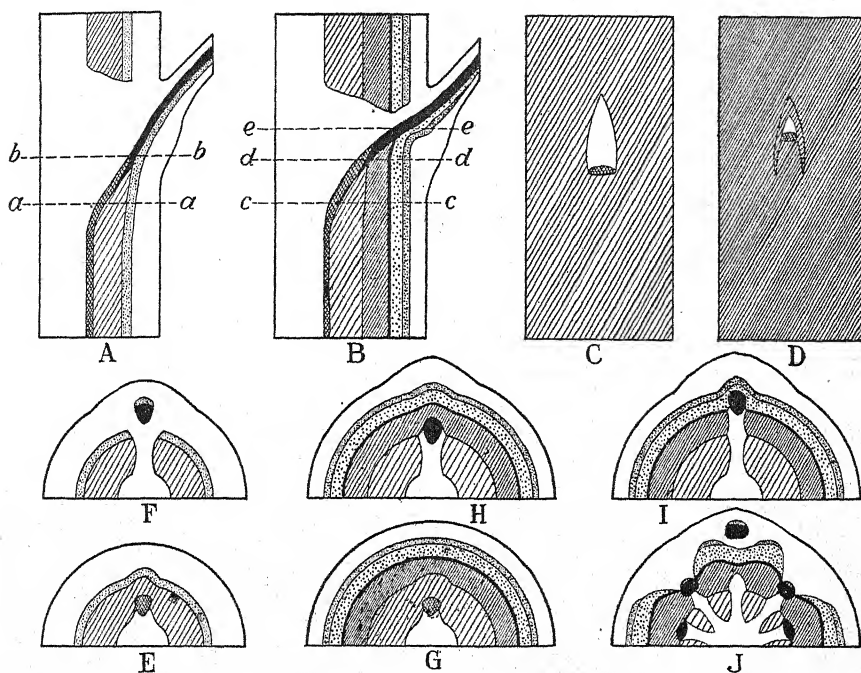


FIG. 65.—Diagrams showing the burial of leaf-trace bases by secondary growth. A, B, longitudinal sections: A, before the beginning of secondary growth; B, after considerable secondary growth; the gap is partly closed and the phloem has been pushed away from the base of the trace, only the xylem being buried. C, D, face views of the surface of the vascular cylinder, the trace cut away at the surface level: C, stage shown in A; D, stage shown in B, the gap partly closed and the base of the trace buried. E, F, cross sections at levels a-a and b-b in A. G, H, I, cross sections at levels c-c, d-d, and e-e in B. J, cross section below a node, showing departure of five traces, the bases buried in varying degrees. (Primary xylem is lightly cross-hatched; secondary, heavily. Primary phloem is finely stippled; secondary, coarsely. The xylem of the leaf trace is not differentiated in kind; its downward continuation is doubly cross-hatched.)

broken. The time of rupture of the trace—its elements dead and non-functioning after the fall of the leaf—depends upon a number of factors: the rate of secondary growth, the size and cross-sectional shape of the trace, and especially the angle at which the trace departs (Fig. 67, B, E, F). The more nearly the course of the trace approaches a right angle with the stem (Fig. 67, E) the longer the period before rupture, since the surrounding tissues are stripped away and the xylem strand

buried. Where the trace passes upward vertically through the cortex, it is quickly broken, owing to the lateral exposure of a long outer part of the trace to the outward thrust of secondary growth (Fig. 67, *F*). Large traces are broken later than small ones, and those crescent-shaped or

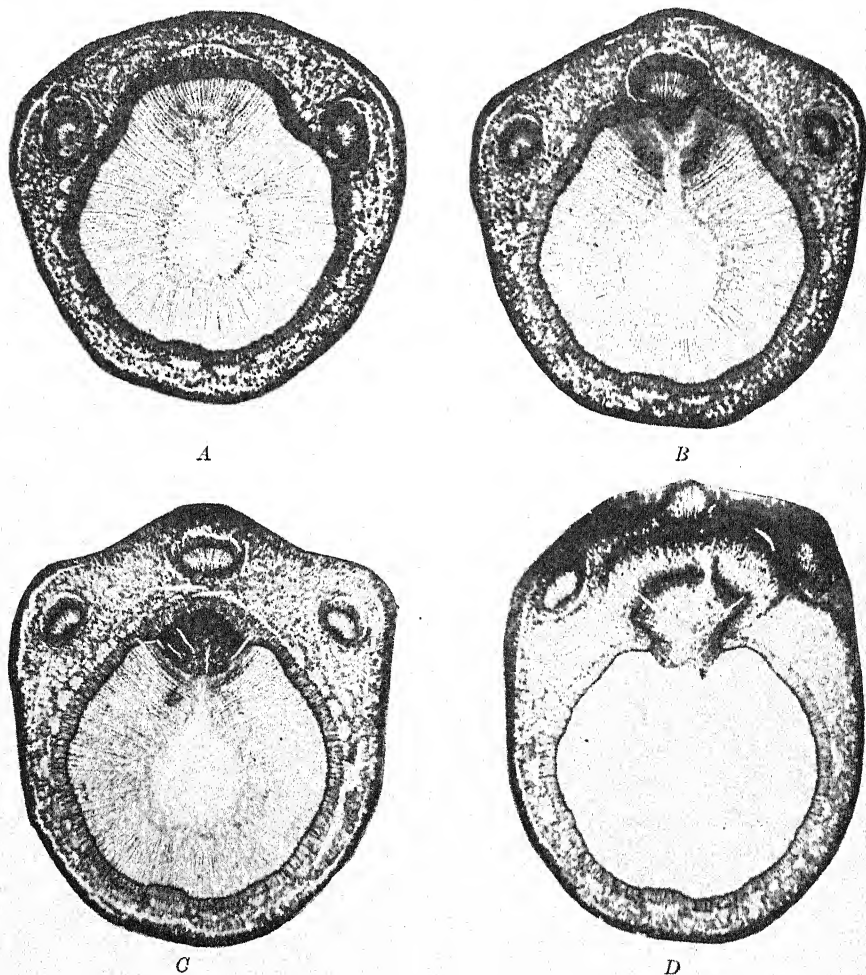


FIG. 66.—Cross sections at successive levels of the nodal region of a one-year-old twig *Pyrus Malus*. *A*, the lateral leaf traces have passed into the cortex and their gaps are closed. *B*, the median trace has passed into the cortex, leaving the gap open; the dark-staining, meristematic branch traces (supplying the bud) are arising from the sides of the gap. *C*, the three leaf traces well out in the cortex; the branch traces have united, the gap is evident. *D*, the leaf traces entering the base of the petiole; the branch traces have formed a nearly complete vascular cylinder.

horseshoe-shaped in cross section later than strap-shaped ones. The inner and outer parts of leaf traces are thus separated (Fig. 67, *G*); the outer part is ultimately lost with the destruction of the cortex, whereas the inner is preserved indefinitely, embedded in the xylem.

In evergreen leaves the traces are extended by a type of secondary growth which increases them in length by additions of new tissue in the middle. The primary xylem of the trace is ruptured, gradually, and in

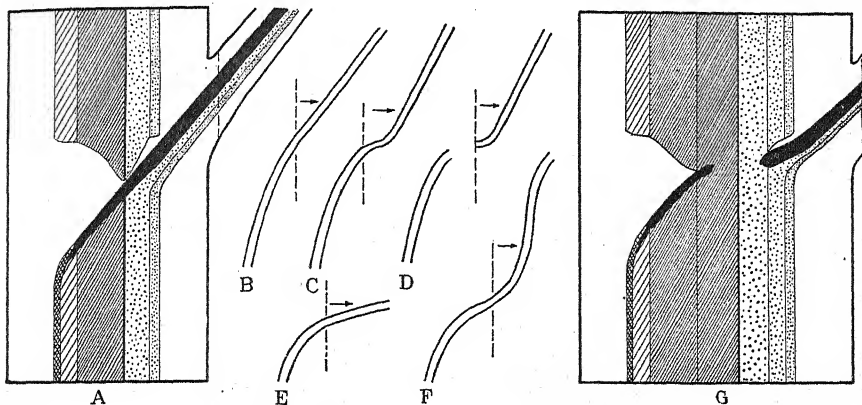


FIG. 67.—Diagrams illustrating the rupture of the leaf trace in deciduous plants. *A*, longitudinal section of node at end of first season's growth; the gap has been closed and the base of the trace buried in secondary xylem. *B*, *C*, *D*, stages in the condition of the trace (other parts omitted) during the following season: *B*, the trace unchanged; *C*, the trace stretched and bent; *D*, the trace broken in two, the outer part carried outward. The dotted lines represent the position of the cambium. *E*, form of trace which ruptures very slowly. *F*, form which ruptures quickly. *G*, longitudinal section of node at end of second season, the trace ends separated by secondary xylem and phloem. (Shading as in Fig. 65.)

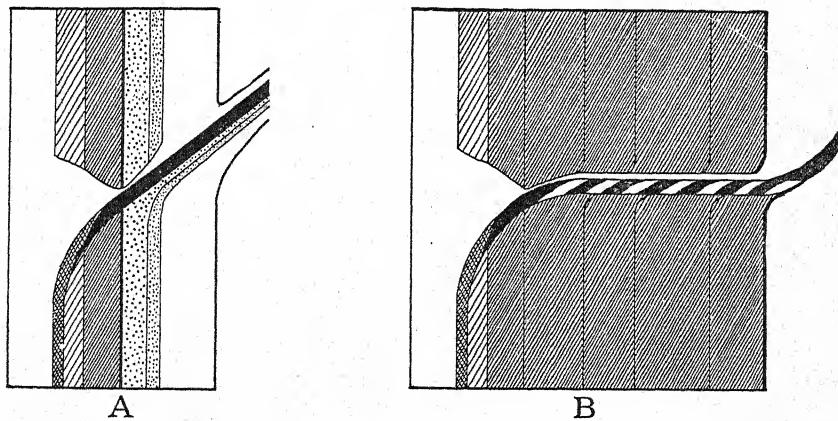


FIG. 68.—Diagrams showing the extension of the trace in evergreen leaves. *A*, the condition at the end of the first season; *B*, at the end of the fifth season (the parts outside the cambium omitted). In *B*, the primary parts of the trace (in solid black) are separated by a central, secondary part (in alternate black and white); this part is ruptured, like the primary, but the breaking is continuous, the trace being built up anew, obliquely, by an "armpit" section of the cambium, an extension along the under side of the trace at the point of its contact with the secondary xylem. (Shading as in Fig. 65. See text for further description.)

an oblique direction, new cells to replace those destroyed being added meanwhile by the cambium of the "armpit" region (Fig. 68). As long as the leaf persists, the upper older xylem cells of the trace are continu-

ously broken and new cells are added below. The gap is often not quite closed, but remains open until the trace is broken. Thus, where the leaves are long-persistent, as in *Araucaria*, the trace may become very long and be evident in secondary wood in annual rings far from the center of the tree. After an evergreen leaf dies there is complete rupture of the trace, as with deciduous leaves. Normally, the ruptured end of leaf traces, both in deciduous and in evergreen plants, is quickly covered by typical cambium cells and there is soon no evidence in the secondary xylem of the position of the trace; but in *Agathis* and *Araucaria* the trace cambium continues to form the trace after the leaf has fallen and secondary wood always shows buried leaf traces.

Branch traces are buried in the same way as are leaf traces. They are, of course, not ruptured. The embedding of branch bases is further discussed later in the chapter.

The Relation of Secondary Growth to Leaf and Branch Gaps.—Leaf gaps are closed by the gradual lateral extension of the cambium, the new meristematic cells arising apparently out of the parenchyma cells of the gap. The size and the shape of the gap determine in part the length of time before the gap is closed, wide gaps being closed more slowly than long narrow ones. In most angiosperms leaf gaps are closed in the first season (Figs. 65, 67). Branch gaps, being often large, are closed more slowly than leaf gaps; some branch gaps remain open until the second to fourth years.

Function of the Cambium.—Meristems which form secondary tissues are commonly looked upon as uniseriate rows of initials which form new cells usually on both sides. Thus the cambium forms xylem internally and phloem externally. The tangential division of the cambium cell forms two apparently identical daughter cells (Fig. 69, B), one of which remains a meristematic cell, the persistent cambial cell; the other becomes a *xylem mother cell* or a *phloem mother cell* (Fig. 69, C), depending upon its position internal or external to the initial. The cambium cell continues to divide in a similar way, one daughter cell in each case remaining a cambium cell, the other becoming either a xylem or a phloem mother cell. The sequence of xylem and phloem formation during this process, if there be any uniform sequence, is not known. It is probable that there is no definite alternation, and it is possible that brief periods of continuous development of one kind of tissue occur. Adjacent cambium cells divide more or less simultaneously to form a tangential row of xylem or of phloem cells. Thus, the row of initials maintains its tangential continuity. In the formation of xylem cells the enlargement of the developing cells causes the outward movement of the cambium and of all cells lying outside of this layer. This, of course, increases the diameter of the cambium cylinder. The maturing of phloem cells causes the outward movement only of the phloem cells and of cells external to these; the

position of the cambium is unchanged by phloem formation. The activity of the cambium, then, causes this meristem to move outward each season to the extent of the thickness of the mature xylem formed in that season.

In plants in which the cambium derivatives are in definite radial rows, a condition found in the gymnosperms and in many angiosperms, it is possible to trace the activities of a given initial throughout the growth of a season. In plants with more specialized xylem and phloem, however, including most of the angiosperms, the elements formed are so diverse in size and shape and gliding growth is so pronounced that, except in the

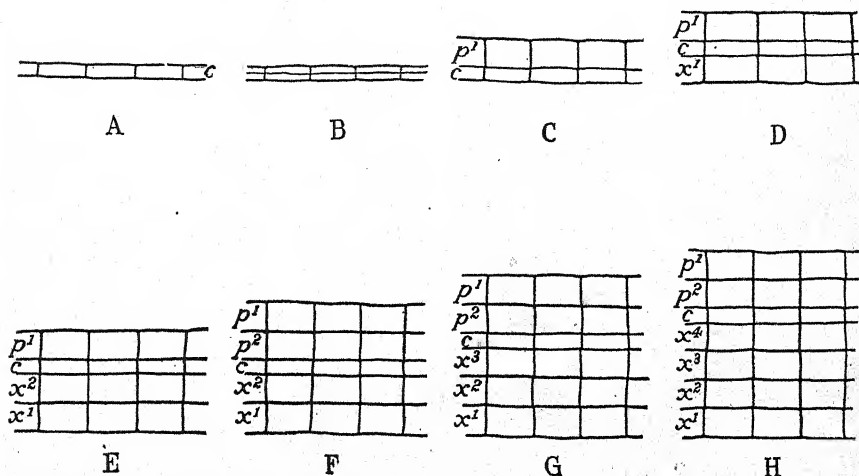


FIG. 69.—Diagrams illustrating the formation of xylem and phloem by the cambium, and the changes in position of the phloem and the cambium brought about by this activity. A, the cambium. B, the cambium cells divided, each forming two daughter cells. C, one daughter cell enlarged and matured as a phloem cell (p^1), the other enlarged to cambium-cell size, remaining a meristem cell (c); no change in the position of the cambium occurs. D, the cambium cells have divided again, the inner daughter cell in this case having matured as a xylem cell (x^1), the outer becoming the cambium cell (c); the cambium and the phloem have been moved outward the width of the xylem cell. E-H, further divisions occur, resulting in the formation of one more phloem cell and three more xylem cells. (The xylem and phloem cells are here represented as maturing before the formation of the next cell, whereas a number of cells are normally present in an immature condition.)

vascular rays, uniform radial arrangement is often not clear. By studying the xylem and phloem of the former type, or the vascular rays in the latter, the ratio of the number of xylem cells to phloem cells formed by the cambium in a given season can be approximately determined. In some cases this ratio is three or four xylem cells to every phloem cell. However, this ratio doubtless varies widely in different types of plants and under different environmental conditions. It can only be said that, in general, several times as many xylem cells are formed each season as phloem cells. This is essentially true of both woody and herbaceous plants.

The Cambium as a Uniseriate Layer.—There exist two general conceptions of the cambium as an initiating layer: one, that it consists of a single row of permanent initiating cells, all cells cut off from which—though they may divide a few times—soon become transformed into permanent tissue; the other, that there are several rows of initiating cells, forming a cambium “zone,” some of the individual rows of which persist as cell-forming layers at least for some little time, giving rise to more than a very few tangential rows of cells. Because cells mature continuously during growing periods on both sides of the cambium, it is obvious that only a single layer of cells can have permanent existence as a cambium (unless there are individual layers for xylem and phloem). Other layers, if present, function only temporarily and become completely transformed sooner or later into permanent cells. The question involved is apparently how many times a xylem or a phloem mother cell and its derivatives may divide; this is difficult to ascertain and seems not to be known. Divisions appear to take place more freely in phloem initials than in xylem initials. (Divisions occurring in a transverse plane, such as those resulting in the formation of wood parenchyma and phloem parenchyma are not here considered.) It seems clear that phloem and xylem mother cells may not divide, or may divide a few times. Perhaps under certain conditions, especially that of very rapid growth, there may be more divisions than under other conditions. The confusion as to the existence of a number of rows of actual cambial cells is doubtless due in part to differences in definition of the term “cambium.” The cambium is commonly looked upon as the initiating layer, but the term is, unfortunately, often loosely applied to the entire differentiating, immature region between mature xylem and mature phloem (Fig. 73). This often leads to the conception that the cambium (in the stricter sense) is a multiseriate layer. Though the term was first applied to a wide layer of differentiating substance, believed to be at least in part without cellular structure, best usage now applies the term not to the entire region, but only to the initiating layer. It is apparent that there is, in most plants at least, but one row of permanently meristematic cells.

Cell Types in the Cambium.—Cambium cells, in general, are of two fundamentally different types: one, the vascular-ray initials, which are more or less isodiametric and give rise to the vascular rays; the other, the elongate, tapering cells which divide to form tracheids, vessels, sieve tubes, and the other vertically elongated elements, in fact, all cells of the vertical system (Figs. 70, 71). The vascular ray initials show little variation in cell shape; the number concerned with the formation of any given ray is few or many, dependent upon the size of the ray, which varies greatly in different species and frequently in the same species. The other class of cells is uniform in shape as seen in cross section, but shows great differences in the proportional relation between length and width as

seen in tangential section. Thus, in woody plants with relatively short cambium cells, as, for example, *Robinia* (Fig. 70, C, D) and *Ulmus* (Fig. 71, B), the length may be from five to ten times the width. In other plants, such as *Pyrus* (Fig. 71, A), *Juglans* (Fig. 71, C), and other types in which the vascular tissues are relatively unspecialized, the ratio of length to width as seen in tangential section may be twenty-five to one, or even greater. The gymnosperms show an extreme condition in which this ratio may be anywhere from fifty to one to one hundred or more to one, dependent upon the species, the age of the plant, and other factors. Herbaceous plants, as a class, do not show great variation in the shape of the cambium cells, the common type being that with the shorter initials. Cambium with short initials is clearly the most specialized type, phylogenetically the most recent.

Size of Cambial Cells.—The actual size of the individual elements of the cambium varies through wide limits. In the specialized woody dicotyledons, such as *Robinia*, the elongate cambium cells of the mature plant are about 175 microns in length by 20 microns in tangential width by 7 microns in radial width. In *Juglans* and *Liriodendron*, which have longer initials, the actual size is about 600 by 25 by 8 microns. The gymnosperms show the extremes of larger size. In *Pinus Strobus*, for example, the dimensions of 4000 by 42 by 12 microns have been given; a maximum length of 5000 microns is reported in *Larix*. The size of the ray initials is fairly uniform, the tangential diameter generally being about the same as or a little less than that of the adjacent fusiform initials. It has recently been shown that, in some groups of plants at least, the length of the fusiform initials increases with the age of the plant. Thus, in the gymnosperms the length may increase from 1 to nearly 4 mm. during the first sixty years, after which it remains constant. In the dicotyledons this increase is much less, being, in unspecialized woody plants, such as *Juglans*, only from 0.8 to 1.2 mm. during the first thirty years. In highly specialized types, such as *Robinia*, this increase may be only from about 0.145 to 0.175 mm. before the maximum is reached. The size of the cambium cells varies to some extent in the same plant, dependent on position relative to branches, buds, or wound tissue, and also with different ecological factors. In crotch angles extreme variation in size and distortion in shape occur. Curly-grained woods are due to abnormalities in the arrangement of the cambium cells or in the form of the cambium cylinder. Spiral grain also is related to the structure of the cambium.

In some woody plants, such as *Robinia* (Fig. 70, C, D) and *Diospyros*, the fusiform cambium cells, as seen in tangential section, are in more or less definite horizontal rows. This stratified arrangement is correlated with short-length initials and with the formation of highly specialized vessels. It is responsible for a similar stratified condition of the cells of

the xylem and phloem. Some genera, for example, *Fraxinus* and *Ulmus* (Fig. 71, *B*), have short cambial initials which are not stratified. This condition is apparently intermediate between the stratified type and the extreme non-stratified type with long narrow initials, such as is found in *Juglans* (Fig. 71, *C*), *Salix*, *Populus*, *Pyrus* (Fig. 71, *A*), etc. The gymnosperms have cambium of the non-stratified type. Herbaceous plants with well-developed secondary growth, as, for example, *Solanum* (potato, tomato, etc.), have short initials that are non-stratified. The prevalent idea that cambial initials are usually brick-shaped is clearly without foundation; it is based upon the study of transverse and radial sections alone.

Structure of Cambial Cells.—As in other meristematic tissues, the protoplast of the cambium initials consists of dense protoplasm without evident vacuoles or stored food. The single nucleus in each cell is well developed, distinct, usually elongate, except in ray initials, and may have several nucleoli. The apparently multinucleate condition seen in tangential sections of the resting cambium is due to the fact that the tangential walls of the radially narrow cells are very thin and transparent, so that the contents of several cells may be seen more or less clearly at the same time. These tangential walls are at all times without definite pits. The radial walls of the cambium cells, on the other hand, are much thicker and, while the cambium is dormant, show abundant pit-like thin spots (Figs. 70, *B*, *C*; 71, *A*, *B*; 91, *C*).

Cell Division in the Cambium.—Division of the cambial initials must provide, of course, both for the formation of new xylem and phloem cells radially on either side, and also in large part for the increase in the circumference of the cambium cylinder itself. The former is accomplished by the tangential division of the cambium initials, and by the subsequent division of the xylem and phloem mother cells; the latter, by typical radial division of the cambial initials in some cases; by transverse division or by oblique radial division followed by increase in size and gliding growth in others; and in part by the increase in the tangential dimension of the initials as the plant grows older. Increase in the number of vascular rays is also an important factor contributing to the increase of the cambium cylinder in circumference. Vascular-ray initials are probably formed from fusiform initials by transverse division of the entire cambium cell, or in some cases of part of the cambium cell only. Longitudinal divisions also occur when the new ray is biseriate or multiseriate. In the formation of very broad and very high rays it is probable that more than one fusiform initial takes part. The increase in the extent of the cambium in a given plant is doubtless due to a combination of the various methods.

Radial division of the cambial initials (Fig. 72, *E*) seems to be characteristic of those plants which have short, stratified cambium cells and in which the derived vascular tissues are of the highly specialized type,

for example, some of the Leguminosae. In plants with longer, non-stratified initials there exist all transitional conditions in respect to the position of the newly formed wall or cell plate, from the transverse plane to the radial-longitudinal plane (Fig. 72, A, B, C). There is evidence to show that in evolutionary specialization the new cell wall tends to approach the radial position as the initials become shortened and approach the stratified condition.

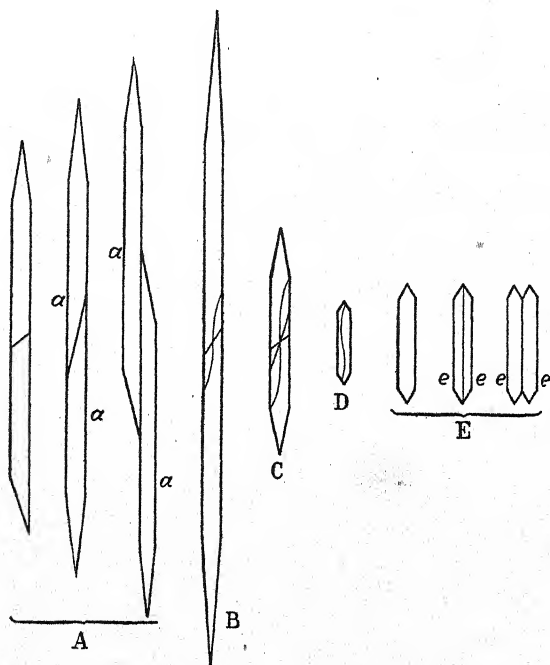


FIG. 72.—Diagrams illustrating the method of increase in girth of cambium. A, fusiform initial dividing pseudotransversely; a, a, products of this division which elongate and slide by one another as they mature (two stages). B, C, D, three kinds of initials, showing types of "radial" (anticlinal) division; B, C, showing two and three types, respectively; D, one type. E, short initial: e, e, the products of radial division of E, which enlarge laterally but not longitudinally. (After Bailey.)

Mitosis in the Cambium.—Recent work on the cambium indicates that mitosis in this tissue involves several unusual phenomena. These are related undoubtedly to the great length of the fusiform initials as compared with their width and are connected with the formation of the cell plate and the division of the cytoplasm. Thus, in the tangential division of the long initials of *Pinus Strobus* the cell plate, in normal cases, is first formed on the spindle fibers between the daughter nuclei after mitosis. This cell plate quickly reaches to the radial walls of the mother cell in the central region, and then extends longitudinally toward its extremities.

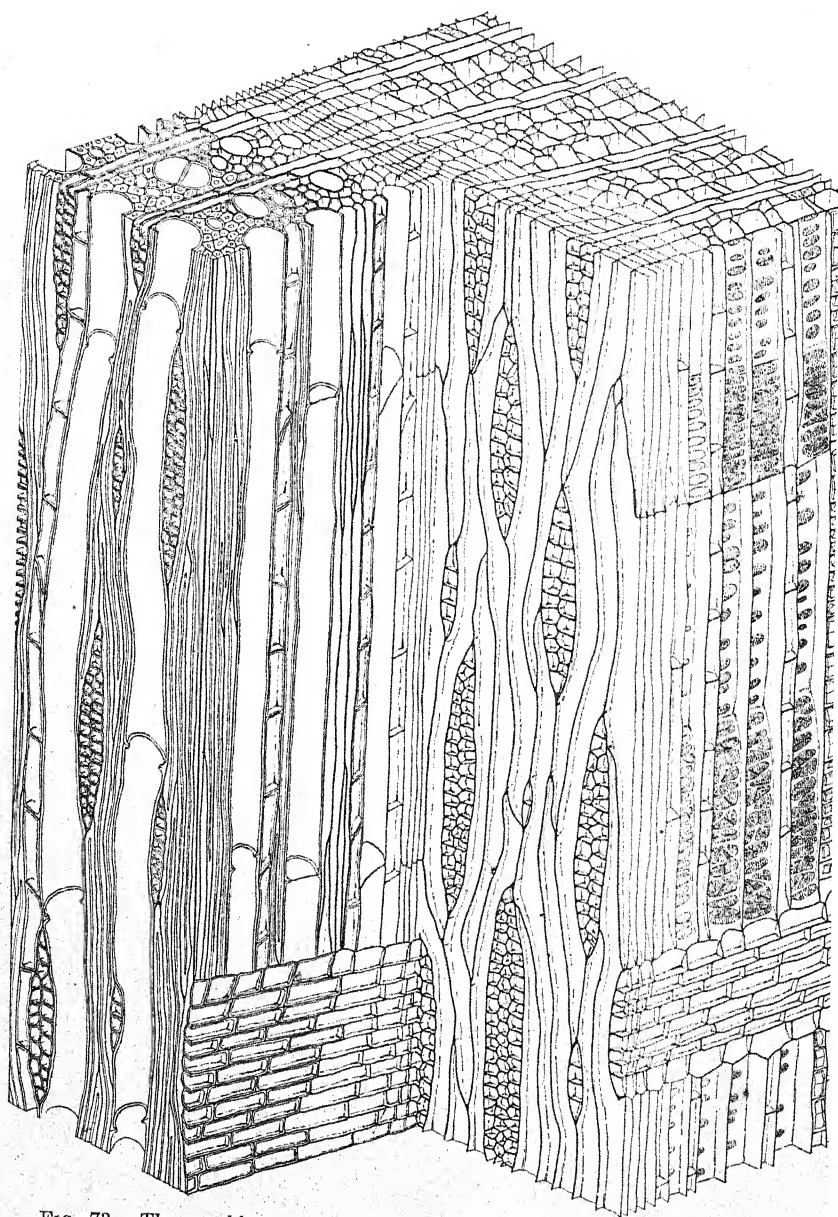


FIG. 73.— The cambium and developing and mature xylem and phloem in *P. Malus*. (The region of maturing xylem is here represented greatly shortened. The tents and the pits of all cells have been omitted.)

After the formation of the cell plate near the nuclei the spindle fibers disappear in that region and further cell-plate formation is carried on toward the extremities of the cell by new groups of spindle fibers ("kino-plasmosomes"), apparently formed from the cytoplasm. As seen in tangential sections of the cambium, these new fibers appear as a "halo" about the edges of the expanding cell plate. Thus in these long cells the entire cell plate is not formed simultaneously, and hence the mother cell is not completely divided into daughter cells at once; the formation of the young wall, dividing the mother cell, is gradual, arising near the center of the cell and extending slowly to its ends.

Gliding Growth of Cambial Cells and of Cambial Derivatives.—According to present views of cambial activity, a very considerable amount of gliding growth is necessary in order that the increase in length of the cambial derivatives be accommodated, and to permit of the general adjustment of cells necessary for the formation of mature xylem and phloem of such a wide diversity of elements as is found in many plants. Also, gliding growth must occur in the cambial cells themselves as the girth is increased. Thus, where a fusiform cambial initial divides transversely, or nearly so, as is frequently the case, it is necessary for the ends of the daughter cells to slide by each other, and by other cells, in order that they may attain their normal size and elongate, tapering shape (Figs. 72, A, B, C; 73).^{*} In some woody plants a part of the cambial derivatives, for example, the wood fibers, may be four or five times the length of the cambial initials from which they were formed; such increase in length can be obtained only by gliding growth (Fig. 74). In cases where adjustment takes place in a transverse direction only, as in the formation of the large, specialized vessels in *Robinia*, *Castanea*, etc., the assumption of gliding growth is not necessary, as it is entirely possible for all adjustments to take place by cell division and growth, and by spatial movement in the zone of plastic cells next the cambium, without the sliding of walls by each other. Gliding growth, may of course, occur here also.

The exact nature of gliding growth is not well understood. The extension of a cell between two other cells, as must occur in the developing xylem of such plants as *Pinus*, necessarily involves the splitting apart of the two cells along the middle line and the consequent rupture of

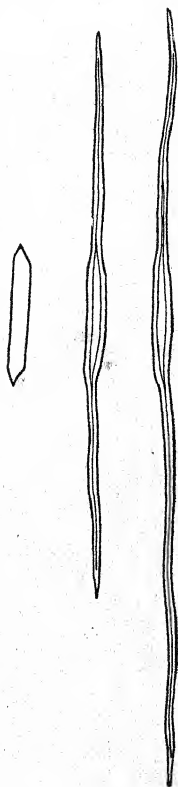


FIG. 74.—Cambium cell and wood fiber (two types) derived therefrom in *Robinia Pseudo-Acacia*. (Drawn to scale.) The elongation of the developing fiber makes necessary the gliding of the tips between cells above and below; see also Fig. 76, A.

existing plasmodesma (if such are present at this stage of development). It must be borne in mind, however, that such splitting is probably not due to mechanical pressure but to something akin to enzyme action or to a growth process. The walls of all cells concerned with gliding growth are still in a very plastic condition, and probably at the time enlargement takes place are still largely protoplasmic in nature. Judging from the fact that half-pits in one cell which do not connect with pits in adjacent cells are never found, it seems certain that pits are not differentiated at the time gliding growth takes place. (Pits in thick-walled cells are structural features largely of the secondary wall, and the latter does not develop until full cell size is attained.) The apparent results of gliding growth could be accomplished if it is assumed that growth in the extending cells takes place at the tips only. By the dissolution of the middle lamellae of the cells on either side by enzyme action, the growing cell could extend between them, laying down new sections of wall upon adjacent walls as its tip progresses. Pit formation could then take place as the secondary wall forms, and plasmodesma connections be reestablished. The latter would then be secondarily formed, a condition perhaps not impossible when the wall is thin and possibly protoplasmic. Such an hypothesis would provide for gliding growth without the necessity of the actual sliding of two walls over each other.

The Ontogeny of Secondary Vascular Tissues.—The xylem mother cells cut off from the cambium may develop into permanent xylem elements without further division, or, as is frequently the case, may divide once or several times before mature tissue is formed. In simple gymnosperm wood all derivatives from fusiform cambial cells become tracheids and are essentially alike except for the differences between spring and summer wood. In wood of this type the tracheids are formed directly from the xylem mother cells by elongation, the thickening of the wall and its differentiation to form pits, and the loss of the protoplast. In such cases the mother cell may or may not divide before maturing. In gymnosperms with wood parenchyma, however, and in all plants containing vessels the xylem mother cells differentiate into two or more cell types, such as tracheids, wood parenchyma, vessels, and wood fibers. Wood parenchyma cells are formed by the transverse division of the mother cell into a number of segments (Fig. 73), and by the subsequent radial enlargement and the thickening of the walls of these segments. The transverse divisions occur in a vertical row of mother cells, so that the resulting parenchyma cells form a vertical series extending for some distance in the axis. In some cases the vertical series of derivatives of a single xylem mother cell retain the prosenchymatous shape of that cell so that the series from a single initial can be readily recognized in the mature tissue. The arrangement of wood parenchyma and its relation to other cells are discussed in Chap. VII.

The Ontogeny of the Vessel.—Vessels are formed from vertical series of xylem mother cells which have been cut off from the cambium initials. Each mother cell becomes a vessel segment by the perforation of its end walls as it matures. In the process of differentiation, the transverse diameter of the mother cell is rapidly increased to the full size of the mature vessel (Fig. 75, A, B, C); and no increase in length occurs. At this stage the vessel appears in longitudinal section as a series of very large cells one

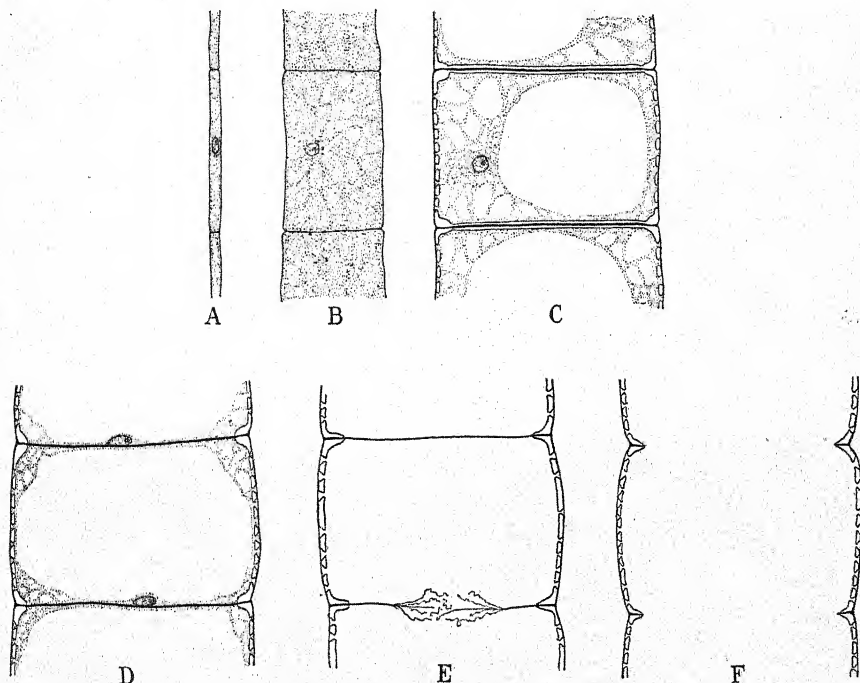


FIG. 75.—The ontogeny of the vessel segment in *Robinia Pseudo-Acacia*. A, the cambium initial. B, the cell much enlarged. C, the cell still further enlarged, the secondary wall well developed, even on the areas later to be removed, and the pits present. D, the cytoplasm restricted to the periphery; the nucleus adjacent to the wall where dissolution is occurring; the secondary wall removed from the pore areas. E, the cytoplasm lost, the very thin end walls disintegrating. F, the mature, perforated, empty cell.

above the other separated by definite end walls which may even have more or less well-developed secondary thickening (Fig. 75, C). Protoplasm and nuclei are still present, though apparently confined to the periphery of the cell. Thus, the vessel segments reach their full size and permanent shape with the walls still unperforated. In *Robinia*, the nucleus of the vessel segment occupies a median position upon the end wall at the stage prior to the dissolution of the wall (Fig. 75, D). This suggests the possibility that the nucleus may be intimately concerned with the formation of the vessel pores. The shape of the vessel segments varies greatly, of course, according to the length of the original cambial

initials and the diameter of the mature vessels. In the wood of *Populus* and in similar woods, the vessel segments are elongated and relatively narrow with oblique end walls. In *Quercus* and *Robinia* the vessel segments may be broader than high with end walls transverse (Chap. IV). In both cases openings are formed through the end walls by the dissolution and absorption of the end wall itself in one or more places. In the formation of porous vessels of the highly specialized type, the central part of the end wall disappears, leaving a narrow rim, or the entire wall may be absorbed. Thus a wide, continuous tube is formed in which the

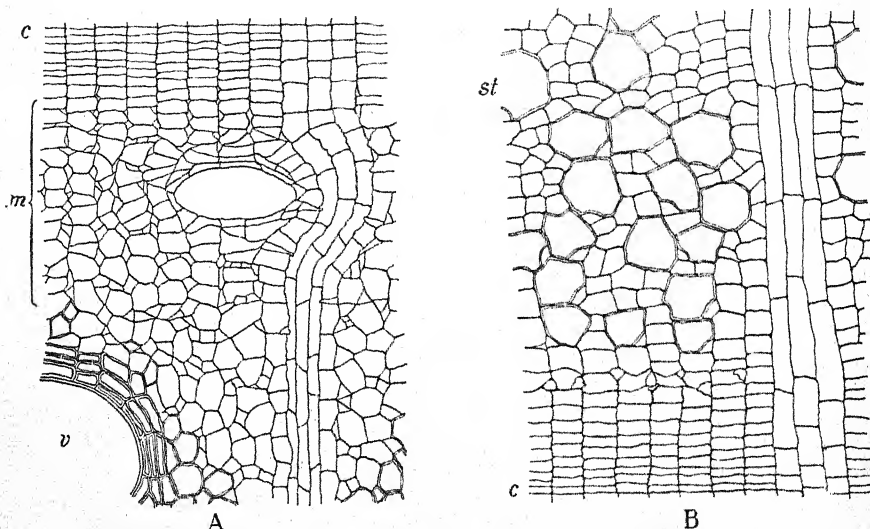


FIG. 76.—The ontogeny of secondary vascular tissue in *Robinia*. A, early stages in xylem formation. c, the cambium. The median portion (m) of the figure shows the region of adjustment to gliding growth, chiefly the result of cell elongation; and of adjustment to vessel development, involving tangential and radial enlargement. The tips of elongating cells appear between the radial rows of cells, increase in size, and crowd the cells from symmetrical arrangement. The great enlargement of vessel segments crowds the surrounding cells from position, flattening and otherwise distorting them; the rays often are turned at right angles to their course. v, a vessel nearly mature, as are surrounding cells. B, stages in phloem development to mature tissue. The companion cells appear early; they and the sieve tubes later enlarge greatly. c, the cambium; st, sieve tube.

vessel segments are to be distinguished only by the vestiges of the end wall which extend a greater or less distance into the lumen. In some herbaceous types where no traces of the end walls of the vessel segments are left, the segments can be recognized by the break in the continuity of the secondary sidewall which occurs between segments, and usually by the somewhat greater transverse diameter of the segments at the middle than at the ends. In scalariform vessels with oblique end walls there may be several openings in an end wall, so that the connection between vessel segments is somewhat restricted by the scalariform bars.

At about the time the openings are made through the end walls the side walls become lignified, and during this process the protoplast disappears.

The enormous increase in the size of the vessel segments as compared with the size of the cambium initials from which they are derived, produces much distortion in the surrounding elements. The cells immediately adjacent to the vessels are frequently much flattened and those farther away crowded out of their original positions. Such adjustment takes place close to the cambium while all cells are very plastic (Fig. 76, A). The movement which occurs as a result of the crowding by the vessel may be likened to movement within a mass of soap bubbles, in which the position and the shape of the bubbles change but no bubbles are broken. In plants with wood fibers that are much longer than the cambium initials, the elongation of the fibers with the consequent gliding growth takes place at the same time as that in which the adjustment to the increase in vessel size is going on.

In many highly specialized woods, for example, *Robinia*, the vessel is the first element of a given region to become lignified. It and the immediately adjacent cells may show apparently complete lignification when the other elements for some distance toward the pith still show cellulose walls. In general, there is no definite order followed in the maturing of the cambial derivatives either as to their position relative to the cambium or as to the types of cells involved.

The maturation of the gymnosperm and angiosperm tracheid and the wood fiber are processes essentially similar to those occurring in the development of the vessel segment. Each differentiates from a xylem mother cell, attains mature size and shape, and then develops a lignified secondary wall. During the last step the protoplast disappears. There is, of course, great variation in the shape and proportions of all these elements in different species, and in the thickness and the pitting of their walls.

The Ontogeny of the Phloem Elements.—The development from the cambium of the different types of cells characteristic of secondary phloem is not thoroughly understood. The scanty evidence available indicates that the process of differentiation in the phloem is comparable with that in the xylem. Phloem mother cells are cut off from the cambium initials. These may divide again or may develop directly into the mature elements. In general, there is apparently more frequent division of phloem mother cells than of xylem mother cells. In the formation of phloem parenchyma the phloem mother cell divides transversely one or more times to form a vertical series (Figs. 71, C, D; 73). These divisions take place very close to the cambium, at least in woody plants, and the series from a given mother cell retains its identity more frequently than is the case with xylem parenchyma. In phloem parenchyma, subsequent differentiation in shape, size, and nature of the wall is very diverse.

In the angiosperms a sieve-tube element and its companion cells are formed from the same phloem mother cell by division in the early stages of differentiation. In some woody plants, and probably generally, the companion cell is cut off from the corner of the phloem mother cell before or as it increases appreciably in size as compared with the cambial initial (Fig. 76, *B*). The sieve tube and its companion cell enlarge in about the same relative proportion, the companion cell usually maintaining its position in the "corner" of the sieve tube, as it were. Herbaceous types and some woody forms are exceptional in this respect, however, in that the mature companion cell does not appear to be closely associated in position with the particular sieve tube to which it is ontogenetically related. The protoplast of the companion cell remains dense, without prominent vacuoles, and retains a well-developed nucleus. In the sieve tube, on the other hand, as the element enlarges, the protoplasm becomes restricted to the periphery of the cell, leaving a large central vacuole. This peripheral layer of cytoplasm persists for a considerable length of time, but the nucleus disappears just before or just as the cell reaches full size and shape. Whether the period of persistence of the nucleus corresponds with that of the functioning of the sieve tube has been questioned. It is generally believed that sieve tubes function for some time after the apparent disappearance of the nucleus (it has been suggested that the nucleus is perhaps still present in a diffused or fragmented condition). Certainly, the cytoplasm is present in normal condition during this time, and crushing of the cells does not occur immediately; also it is unlikely that the period before full size is attained is the functioning period of such cells.

The development of the perforations of the sieve plate has been studied in considerable detail. In its early stages the sieve plate is a cellulose plate traversed by plasmodesma strands. These strands enlarge and at the same time the size of the perforations through which they pass is increased by dissolution of the surrounding wall. In plants with large sieve pores, as, for example, most of the angiosperms, several of the plasmodesma strands may fuse, by removal of the separating portions of the wall, to form a protoplasmic rod extending through the pore. A large pore of this type therefore represents morphologically a sieve field. In the mature element, this protoplasmic rod becomes perforated through the center by an extension of the central vacuole. Thus, the sieve pore becomes an opening between the two adjacent elements and is lined with a protoplasmic sheath continuous with the cytoplasm of the elements on both sides and through which the vacuoles are united. Hence, as is seen in many cases, slime plugs (Chap. VIII) may extend through the openings. The formation of the sieve pores in the gymnosperms is very similar to that in the angiosperms, the chief difference being that in the former the pores are much smaller and the strands passing through them

represent individual plasmodesma. Here each sieve field has many perforations.

Just as an angiosperm vessel is formed from a series of xylem mother cells, so a sieve tube with its companion cells is developed from a vertical series of phloem mother cells, each mother cell forming a sieve-tube segment. In the gymnosperms, inasmuch as the sieve tubes are not joined in vertical series, and companion cells are wanting, the sieve-tube cells are formed directly from the phloem mother cells. The sieve fields in these cases are upon the sides of the sieve-tube elements.

Phloem fibers arise from phloem mother cells in the same way as wood fibers are formed from the xylem mother cells. Stone cells in the secondary phloem are usually derived from phloem parenchyma or from phloem ray cells, and this change occurs rather late in the existence of the tissue concerned.

The Ontogeny of Vascular Rays.—The formation of xylem and phloem rays from the vascular-ray initials takes place by the differentiation of the derivative cells of the cambial initials directly into mature elements, probably without additional divisions. The whole matter of the development of secondary tissues from the cambium is much in need of further critical study.

The Time of Cambial Activity.—In all plants with perennial axes which have an annual dormant period, and especially in the woody plants of the temperate zones, periodicity in the activity of the cambium sets off the xylem formed in any one year from that of the previous and the following year. Such layers of tissue are called annual rings (Chap. VII), since one ring only is formed each year. In the phloem, however, there is no similar definitely limited layering formed by such periodicity (Chap. VIII). The beginning of division among cambial cells after the winter dormant period takes place in early spring—in the northeastern United States in April and May—before, during, or after the development of the leaves. In evergreen trees it may occur somewhat earlier. There is little or no uniformity in the position of first growth in the plant, this being often in the central part of the tree, extending thence to all parts, but cambial growth may also start at the base of the tree or even in the twigs. Likewise, of two trees of the same species growing side by side, one may possess cambial activity while the other is still dormant. On bright, sunny days in late winter, cambial activity may be started on the southwest side of exposed trunks as a result of absorption of heat from the sun by the dark-colored bark. If such conditions are followed by a rapid temperature fall, the active cambium cells are likely to be killed, and the type of winter injury known as “sun scald” results.

There is evidence to show that the cambial derivative cells first to mature in the spring are phloem mother cells. Of these, at least a part are cells which were cut off from the cambial initials during the previous

season and have remained over winter in an immature condition. Thus, new sieve tubes are formed at a time when the translocation of stored food materials is very actively going on. From histological evidence, it seems probable that in some woody plants all sieve tubes functioning in a given season are matured during that season, all sieve tubes matured the preceding season ceasing to function permanently in the fall, though they may not lose their protoplasts or become crushed until rapid growth begins in the spring. The period of most rapid phloem formation may come several weeks after the differentiation of the first phloem elements. This period coincides, in general, with that of the most active xylem growth. The duration of cambium activity varies with different ages of the plant and of the plant parts, with different species, and with environmental conditions. Generally, after the "flush" of growth in the early summer there is a gradual slowing down in the formation of new cells, and in the trunk and main branches of some species there is cessation of cambial growth by midsummer. Cambial activity continues longest in the small rapidly growing twigs or shoots that are late in completing their apical growth. In nursery trees, growth in diameter may continue until late in the fall; in such cases terminal growth also usually continues late. Abundant nitrogen and water in the soil are apparently important causal factors in such late growth.

The Burial of Branch Bases.—As successive annual rings of xylem are laid down by the cambium, all tissues within the cambium cylinder are buried more and more deeply. Thus the bases of branches become embedded in the wood of the tree trunk. In a living branch, the buried portion has the shape of an inverted cone, because, as new layers of xylem are laid down over the branch, the cambium is moved by the increase in the diameter of the trunk (Fig. 77) farther and farther away from the point of insertion of the branch in the trunk. The buried portion of the branch cannot increase further in diameter; hence the inner portions are progressively of less and less diameter as the attachment to the primary cylinder is approached. At the apex of the cone-shaped mass thus formed, is the pith of the branch at its point of union with the pith of the main axis (Fig. 77, A). When a branch dies, it ceases, of course, to increase in size and may be buried as a cylinder of dead tissue. Knots found in lumber are embedded branches. The knots are loosely or tightly attached to the board, depending on whether the branch was dead or living at the time it was embedded.

As the base of a branch is buried by the formation of new xylem on the main axis, the phloem tissues about its insertion are forced outward—those in the angle of the crotch more rapidly—so that the base of the branch is stripped of its phloem. In small branches in which the increase in diameter is relatively small as compared with that of the main axis, as in the fruit spurs on the larger limbs of apple trees, this stripping is most

marked. In this process the phloem tissues are thrown up into folds which often appear as concentric rings about the base of the partly buried branch. With larger branches and more rapid growth, the older

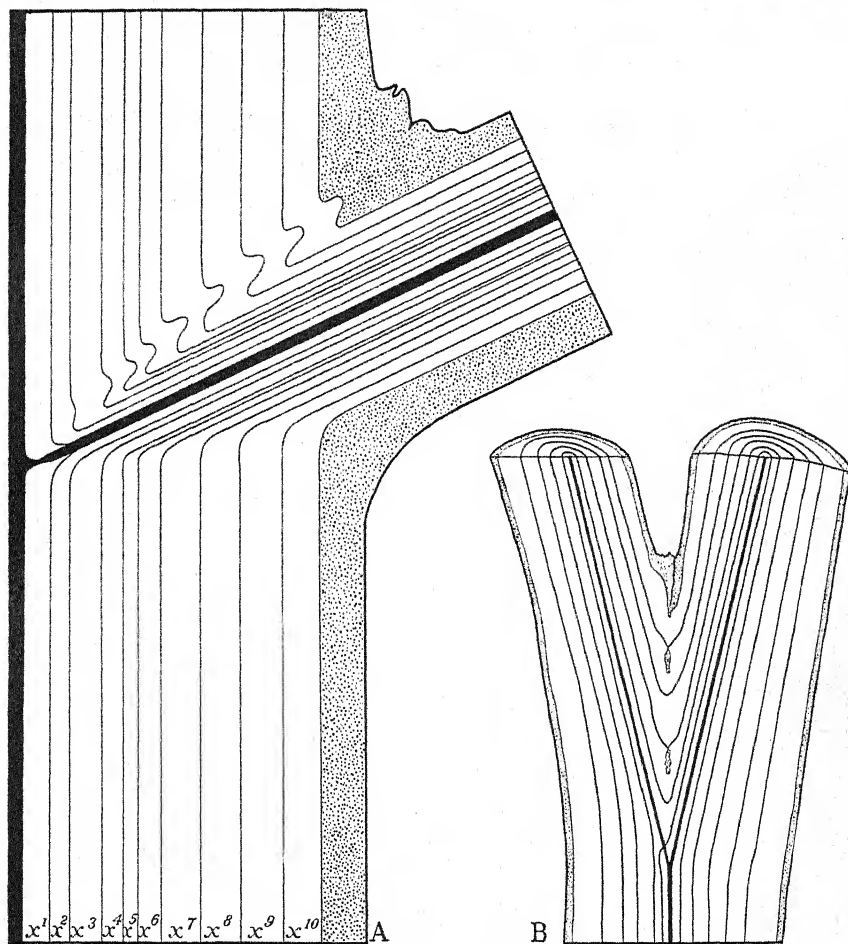


FIG. 77.—A, diagram illustrating the burial of branch bases by secondary xylem. The phloem is pushed away from the buried portion and thrown up in the crotch angle into folds. The cambium layer is also distorted in position. The pith is shown in solid black; the phloem and cortex stippled. x^1 to x^{10} successive annual rings. B, diagram of crotch with narrow angle, showing union of xylem of trunk and branch, the pushing out of the phloem in the angle, and the occasional enclosure of "pockets" of phloem within the xylem. The latter condition, together with the formation of abundant wood parenchyma in the xylem of the crotch union, renders the crotch weak. (B, after MacDaniels.)

phloem is mechanically broken and crowded out of the crotch angle, and the younger, more plastic tissue is thrown up into irregular folds. Apparently, none of the cambium is destroyed in the process, but great distortion in the shape and arrangement of the cells results. Adjustment to

the necessary shortening of the cambium in the crotch angle probably takes place during the growing season while the cells are in a plastic condition. At this time some of the cells are apparently forced laterally out of the crotch angle to the sides of the crotch where they help to compensate for the increase in the girth of the cambium which takes place in this region. Gliding growth may, of course, also be involved in these adjustments.

In the crotch angle there is usually a well-defined region where the tissues of the trunk meet those of the branch. Here the conducting tissues of branch and trunk may remain more or less distinct, and, between the two, masses of thick-walled parenchyma may be formed. Thus the branch is not "tied to" the trunk on the upper side, and as a result there is in the angle of many crotches a zone of weakness which may cause the branch to break away when under stress. Where the angle of the crotch is very narrow and growth is rapid, the bark on the two sides is forced together before cambium growth in the angle pushes it out beyond the region of xylem union. "Pockets" of dead phloem are then enclosed in the angle (Fig. 77, B), and are another cause of weak crotch union. The nature of the crotch tissue, the angle at which the branch meets the trunk, and the relative size of trunk and branch all have a practical bearing in the practice of pruning fruit trees.

✓ **Cambium Growth about Wounds.**—Among the important functions of the cambium is the formation of *callus*, or *wound tissue*, and the healing of wounds. When wounds occur in roots or stems, masses of soft parenchymatous tissue quickly form on or below the injured surface; this tissue is known as "callus." Callus may be formed by the division of parenchyma cells in the phloem and the cortex, but its most frequent source is the cambium. In the formation of callus in the healing of a wound there is at first abundant proliferation of the cambium cells, with the production of masses of parenchyma. The outer cells of this tissue either become suberized themselves, or periderm (Chap. IX) develops within them, so that a protecting bark is formed, beneath which the cambium is active in forming new vascular tissue in the normal way. In the case of pruning wounds, callus is formed about the edges early in the growing season. As a new annual ring is formed in the uninjured surrounding tissues the cambium layer assumes a position at an angle to the face of the wound at the point of intersection with it. In this position new tissue formed in the normal way will extend the growing layer over the cut surface until the two opposite sides meet. The cambium layers then unite and the wound is completely covered. Subsequently formed annual rings serve but to bury the wound more and more deeply.

✓ **The Cambium in Budding and Grafting.**—The important practices of budding and grafting have as their basis the ability of the cambium of both stock and scion to develop callus and unite, thus forming over the

union of stock and scion a continuous cambium layer which will give rise to normal conducting tissue. In such cases there is apparently an actual union of the cambium of the two plants. In cases of so-called incompatibility of stock and scion, such as occurs between some varieties of apple and certain dwarf-apple stocks, the cambium of the stock and scion do not unite to form a normal growing layer which will, in turn, produce normal xylem and phloem, but produce, instead, masses of parenchyma which make the union weak and conduction slow. The whole matter of cambium activity and structure in relation to the graft union needs further careful study.

Where the cambium is injured during the growing season, as, for example, when branches are ringed, the cambium may be regenerated from the immature xylem cells beneath, provided the tissues are protected from desiccation soon after the injury. Thus, in ringing experiments, it is sometimes difficult to prevent the formation of new cambium even by scraping the surface of the wound with a knife. In such cases callus tissue is formed by the living, immature cells in the xylem, and in this callus a new cambium is differentiated. At first, this new meristematic tissue is not normal cambium in shape and size of cells, but eventually the normal condition is attained. The formation of galls and some types of burls may be due to local stimulation of the cambium to abnormal activity by insects or disease. Such phenomena are largely pathological and a discussion of them has no place here.

The Cambium in Monocotyledons.—The monocotyledons as a class are without secondary thickening, the plant body consisting of primary tissue only. Vestiges of typical cambial activity occur, however, in not a few genera, especially in the vascular bundles of nodal regions and of leaf bases. A special type of secondary thickening occurs in a few forms (some of the tree-like, or woody Liliaceae, *Dracaena*, *Aloë*, *Yucca*, etc., and some palms and other forms), whereby the stem is increased in diameter by the formation of a cylinder of new bundles embedded in a tissue of less-specialized nature (Fig. 78). Here a cambium layer is formed from the meristematic parenchyma of the pericycle or of the innermost cortical cells. The initials differ from those of the gymnosperm and angiosperm cambium in that they are much shorter in proportion to their width and are not prosenchymatous in shape. The type of secondary tissue formed in the monocotyledons is also very different from that formed in the other groups. The cambium does not produce phloem on the outside and xylem toward the inside in the normal way, but forms on the inner side amphivasal or collateral bundles, scattered in parenchymatous ground tissue. The extracambial tissues formed are very small in amount and parenchymatous in nature, or are lacking. In the cambium layer proper, tangential division takes place for the most part. In the subsequent specialization of these cells to form the xylem

and phloem of the bundles, however, division takes place first in the radial, and then in all planes (Fig. 114).

The thickening which takes place in the bases of some palm stems is not due to the activity of a definite cambium layer, but is, rather, the result of gradual increase in size of cells and of intercellular spaces, and, in rare cases, of the proliferation of strands of tissue to form new fibers; that is, it is, in general, a long-delayed continuation of primary growth. Usually no new vascular tissue is formed in the thickening of the palm

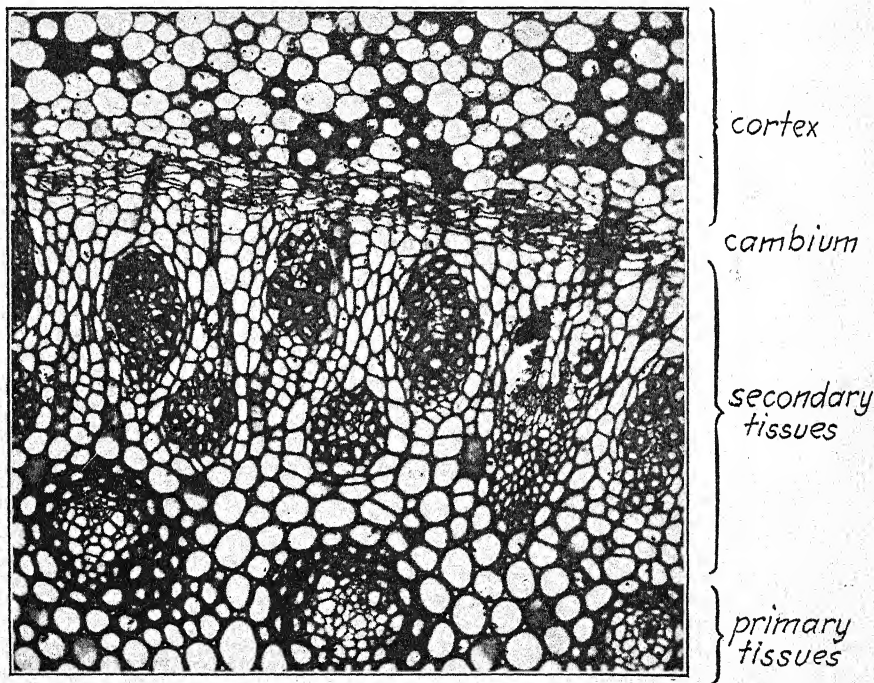


FIG. 78.—Special type of cambial growth of "woody" monocotyledons; stem of *Dracaena fragrans*.

stem, though in some genera secondary growth of the type just described does occur.

The development by cambial activity of steles with anomalous structure is discussed in Chap. XI.

References for Chap. VI

(See also References for Chap. V)

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CHAPTER VII

SECONDARY XYLEM

Secondary xylem often makes up the bulk of the vascular tissue of a plant, and, in most woody plants, constitutes the bulk of the entire plant body. In such plants it is a tissue of great importance, because through its functions a huge plant body may be maintained in the atmosphere with its various parts favorably situated as to light and air. Mechanically, the xylem supports and anchors the body; physiologically, it conducts water, and perhaps other inorganic materials absorbed by the roots, to all living parts of the plant. Further, it provides in its living cells storage space for considerable quantities of food. Of the total amount of xylem in the body of most trees, however, a considerable part (heartwood) is not functioning except in the way of mechanical support. The secondary xylem of tree trunks is of great economic importance, since it constitutes the timber and wood of commerce. It also has many other uses of less, though often of much importance.

GROSS STRUCTURE OF SECONDARY XYLEM

Secondary xylem consists of a closely compacted mass of thick-walled cells so arranged as to form two systems; a longitudinal, that is, vertical, and a transverse, radiating system.¹ The longitudinal system consists of elongate, overlapping, and interlocked cells—tracheids, fibers, and vessels—and of longitudinal rows of parenchyma cells. All these cells have their long axes parallel with the long axis of the bundle or central cylinder of which they are a part. The radial system consists chiefly of parenchyma cells with their long axes at right angles to the long axis of the central cylinder. These horizontally elongate cells constitute the xylem rays.

Xylem Rays.—*Xylem rays*, or *wood rays*, are sheets of tissue, more or less strap-like or ribbon-like, extending radially in the xylem (Figs. 79, 80). As series or systems of conducting tissue, such cells are not confined to the xylem, but extend as continuous bands through the cambium into the secondary phloem, where they form a conspicuous and functionally important part of that tissue also. These radiating strips of cells are generally known as *medullary rays*, or *pith rays*, since in position and in

¹ The distinction of two such systems in secondary xylem is made merely for convenience in description. As distinct tissues, the systems, of course, do not exist. The basis of distinction is that of arrangement of cells and of direction of conduction.

their parenchymatous nature they to some extent suggest radiating portions of the pith. The use of this term is due also to a supposed homology of these structures with actual projections of the pith (medulla), such as occur in herbaceous stems of the *Ranunculus* type (Fig. 112, F). The term "medullary ray" for these radiating bands of the xylem and phloem is, however, clearly a misnomer, since in the majority of cases these rays of tissue have no connection with the pith, and, further, are not morphologically homologous with structures, such as the radiating pith "arms" of stems of the *Ranunculus* type, which may perhaps logically be called medullary rays. Hence, it seems that, in spite of the long-standing and almost universal usage of the term, it is best that it be not used in the sense of rays of vascular tissue. Of terms which may supplant "medullary ray," *vascular ray* appears to be the best. This has the disadvantage of being a new term, but is accurately descriptive, since the bands are rays of vascular tissue, partly of xylem, partly of phloem. The terms *wood ray*, or *xylem ray*, and *phloem ray* for those parts of the ray confined to xylem and phloem respectively, are already in use and are particularly appropriate.

Vascular rays lie at right angles to the long axis of the stem or root, and are continuous in all cases through the cambium and into the phloem. They are straight except when crowded aside by unequal growth of the surrounding cells or tissues. All vascular rays are initiated by the cambium, and, once formed, are increased in length indefinitely by the cambium. New ray tissue is thus added in a region near the middle of the ray, the older portions being pushed apart by the formation of new cells in the cambium between them. The length of a ray thus depends upon the length of time since it was initiated, and upon the rate of growth of the secondary tissues. At the beginning of secondary growth a certain number of vascular rays are initiated. These rays, however, become more and more widely separated in the new distal parts as the circumference of the vascular cylinder rapidly increases with the addition of new secondary tissues. Soon the width of the segments of xylem and phloem so increases that the cells formed in the center of the segments are remote from the existing rays. New rays are then formed at frequent intervals tangentially, so that all xylem and phloem cells are fairly close to rays. In elongate cells, such as tracheids, the scattered vertical distribution of the rays (Figs. 79, C; 83, C) brings at least a part of each cell near a ray. In gymnosperm woods where no wood parenchyma is present, every tracheid is probably thus brought into direct contact with a wood ray. Vessels, also, in their longitudinal extent, come into contact with rays. In herbaceous stems, such as those of *Ranunculus*, where vascular bundles are separated by projecting parenchymatous wedges (which may perhaps be called true "medullary rays"), and in vines, such as *Clematis*, where the bundles are separated by bands of secondary

parenchyma, vascular rays are lacking. In such cases the bundles are so small that no conducting cells are far removed from radial sheets of parenchyma. The absence of vascular rays in such cases is doubtless due to loss during evolutionary specialization. The relation of contact or of closeness in position of living cells (ray cells or wood parenchyma) to conducting cells (tracheids and vessels) is apparently of the greatest importance to the functioning ability of these non-living cells.

Annual Rings.—The longitudinal system itself shows no conspicuous gross structural features. The complete cylinder of secondary xylem is, however, commonly seen to consist of concentric layers (Fig. 3), each one of which represents the annual increment of wood. When seen in cross-section of the axis, these cylindrical layers appear as rings; hence the term *annual ring* is applied to the layer formed in a year. An annual ring is, therefore, the layer of secondary xylem formed in a year over the entire plant, and is, hence, an extensive tubular structure having the general form of the axis of the plant. It is open at the ends where meristems occur. The term "annual ring" should not be applied to the line separating the wood formed in two successive seasons.

The width of annual rings varies greatly and depends upon the rate of growth of the tree, which is, of course, controlled by many factors. Wide annual rings are formed in young trees and under favorable growth conditions generally. Unfavorable seasons produce very narrow rings, and favorable seasons wide ones. Such injury as defoliation during the growing period also causes narrow-ring formation. Abrupt changes in the width of rings successively formed are produced by sudden changes in the growth conditions of the tree; serious accident to the tree, severe pruning, changes in soil drainage, fertilization, removal of shading trees, etc. leave evidence of the changed conditions in the width of the ring. Thus, the annual rings of the tree provide a very real record of some phases of the history of the tree.

An annual ring varies in width in different parts of the plant and in different parts of the circumference of the axis at a given level. The thickness around the axis is most uniform over parts that are free from branches, as the smooth trunks of trees. Below the insertion and along the underside of branches, in some types of crotches, above large roots, about wounds and other abnormalities, there may be a very decided thickening of the ring. Local increased food or water supply is apparently responsible for this condition. In trees, such as the apple tree, with prominent large branches low on the trunk, the trunk may be built up in definite ridges or segments, each composed of the conducting tissues leading to the limb directly above. Where there are several large limbs near the same level, the entire trunk below may be divided into indefinite radial segments of tissue leading mainly to those limbs. The upper central part of the tree may thus be robbed of sufficient water and

nutrients. The segments are, of course, not distinct except as flutings on the stem, and merge into one another laterally. Experiments have shown that, even in smooth trunks, conduction is more or less restricted to vertical segments of the trunk; that is, roots on one side of a tree to a large extent supply the branches on the same side. Conduction laterally is slow in the trunk, the "main current" passing directly upward. Tangential conduction takes place where no roots or branches occur on one side, as well as where wounds cut off direct communication. But-tressed tree trunks, such as are seen in elm trees and in many others, especially tropical forms, are due to strong local thickening by the cambium above the main roots.

Annual rings are characteristic of woody plants of temperate climates; they are weakly developed or lacking in tropical forms except where there are marked climatic changes such as distinct wet and dry seasons. Annual plants and herbaceous stems of perennials show, naturally, but one layer.

Spring Wood and Summer Wood.—The presence of annual rings is due to seasonal conditions, the tissue formed in the spring, *spring wood*, being more or less different in cell size, cell type, and cell arrangement from that formed in the summer, *summer wood*. (The terms *summer wood* and *fall wood*, formerly used for spring and summer wood respectively, have ceased to be used, since in most trees no wood is formed in the autumn, and wood is commonly developed in the spring.) An annual ring, therefore, consists of two parts, an inner layer, spring wood, and an outer one, summer wood. However, no line exists between these two parts of the ring, since spring wood merges into summer wood, just as one season gradually passes into the other. The line between the summer wood of one year and the spring wood of the next year is, however, sharp, and it is this line which renders the annual ring distinct.

False Annual Rings.—The formation of *false annual rings* frequently occurs as the result of a check of normal development of xylem followed in the same season by a resumption of growth. Defoliation by insects, hail, etc., also drought and other disturbances of development, cause "summer" wood to form prematurely. In trees with determinate growth, such as the oak, the winter buds, especially the terminal buds, may begin growth prematurely in late summer; the consequent growth activity is accompanied by the formation of a false annual ring. False rings may be readily detected by the less sharp delimitation at the outer edge of the summer wood.

Ring-porous and Diffuse-porous Wood.—Annual rings are often rendered more conspicuous by the restriction of vessels to the spring wood, or by the formation there of much larger vessels, as in *Quercus* (Fig. 82, A), *Catalpa*, *Ulmus* (frontispiece), or of more numerous and larger vessels there than in the summer wood. When, for these reasons,

xylem shows the spring wood conspicuously distinct from the summer wood, it is said to be *ring-porous*, as in *Fraxinus* and *Quercus* (Fig. 82, A); when the vessels are fairly uniformly scattered through the ring, as in *Betula*, *Acer*, and *Populus* (Fig. 81, A), and where the transition in size or abundance is very gradual from the early-formed to the late-formed cells, as in *Juglans* and *Pyrus* (Fig. 83, A), the wood is called *diffuse-porous*. Between these two types no line can be drawn and many woods are of distinctly intermediate type in this respect. The type of vessel occurring in the wood bears no relation to the ring-porous or diffuse-porous condition.

GENERAL HISTOLOGICAL STRUCTURE of SECONDARY XYLEM

Cell Types and Cell Arrangement in Secondary Wood.—In both the longitudinal and radial system living and non-living cells occur, the proportions and the arrangement of the two kinds varying greatly with the species, and to some extent also with the time of year when formed, with the organ in question, and with the individual plant. The radial system, that is, the wood rays, consists in most plants wholly of living cells; the longitudinal system, on the other hand, commonly possesses a rather small proportion of living cells. These, in the form of wood parenchyma, make up longitudinal, uniseriate strands of cells placed end to end, extending indefinitely in the wood (Figs. 80, C; 82, B). The water-conducting and the supporting cells of the different types occur in various proportions and arrangements. Usually, in a given wood only a few kinds of cells are present, but some species possess several cell types. In *Abies*, for example, the wood (with the exception of the wood rays) consists wholly of tracheids, or, in some species, of tracheids and wood parenchyma; in *Picea*, of tracheids and fiber tracheids, and in some species of wood parenchyma also; in *Larix*, of tracheids, fibers, and wood parenchyma; in *Liriodendron*, of vessels, fiber tracheids, and wood parenchyma; in *Acer*, of vessels, fibers and wood parenchyma; in some species of *Quercus*, of tracheids, fiber tracheids, typical fibers, libriform fibers, mucilaginous fibers, vessels, and wood parenchyma. (For description of cell types see Chap. IV.)

The different cell types are arranged in various manners. (The radial arrangement of all cells is, of course, the result of the method of development of secondary tissues.) The cell types may be fairly uniformly distributed through the wood (Figs. 81, A; 84, A), or there may be formed a somewhat definite pattern of rows and masses of the different types (frontispiece). More or less definite tangential rows constitute a frequent type of arrangement; for example, in *Carya* and *Diospyros* (Fig. 84, A), the wood parenchyma cells are thus placed (in the figure the parenchyma cells are the small cells with large lumina). Vessels are often found in clusters, as in *Betula*, *Ulmus* (frontispiece), and *Robinia*.

Wood Parenchyma Distribution.—The distribution of wood parenchyma occurs in ways which are very uniform and constant in genera and in larger groups. This distribution is of three types. In some gymnosperm woods, wood parenchyma is absent; in others, such as that of *Larix* and *Pseudotsuga*, and in some angiosperm woods such as *Magnolia* and *Salix*, wood parenchyma cells occur only in the last-formed tissue of the annual ring,—in other words “on the face of the summer wood.” Such woods have *terminal wood parenchyma* (Fig. 85, A). In cases where parenchyma occurs not only in this location, but is also scattered more or less throughout the annual ring, some of the parenchyma cells lying among the tracheids and fiber tracheids, the plant has *diffuse*, or *meta-tracheal*, wood parenchyma (Fig. 85, B). *Pyrus* (Fig. 83, A), *Quercus* (Fig. 82, A), and *Diospyros* (Fig. 84, A) have diffuse wood parenchyma. Where parenchyma occurs at the edge of the annual ring, and elsewhere

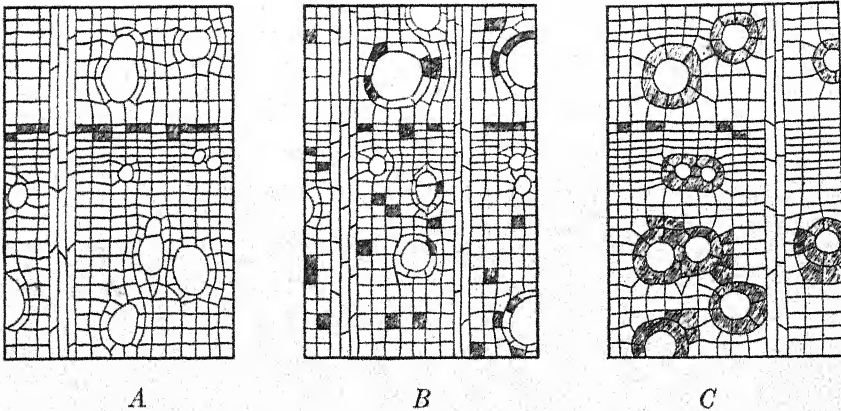


FIG. 85.—Diagrams illustrating wood-parenchyma distribution, the parenchyma cells shaded. A, terminal; B, diffuse; C, vasicentric.

only about vessels, that is, in direct contact with the latter, or in contact with other parenchyma cells which are directly or indirectly in contact with vessels, and does not occur isolated among tracheids and fibers, the plant has *vasicentric*, or *paratracheal*, wood parenchyma (Fig. 85, C). *Acer*, *Fraxinus*, and *Catalpa* have parenchyma of the latter type.

Structure of Gymnosperm Wood.—Certain general types of secondary xylem characterize the larger plant groups. That of the gymnosperms is simple and homogeneous, consisting of very few cell types, often of tracheids only—with the exception, of course, of the rays—as in species of *Abies* and in *Agathis*. In such xylem the summer wood differs hardly at all from the spring wood; in other cases, as in *Larix*, *Sequoia* (Fig. 80, A), and in the hard pines, the summer wood is conspicuously different from the spring wood. Other genera show intermediate conditions. In all cases the non-living cells of the summer wood, being fiber tracheids or

fibers, differ from typical tracheids only in thickness of wall, width of lumen, and capacity for conduction. Typical fibers are rare in gymnosperm woods. Wood parenchyma, often called resin cells in gymnosperm wood, is absent in a few genera, for example, *Araucaria*, *Taxus*, species of

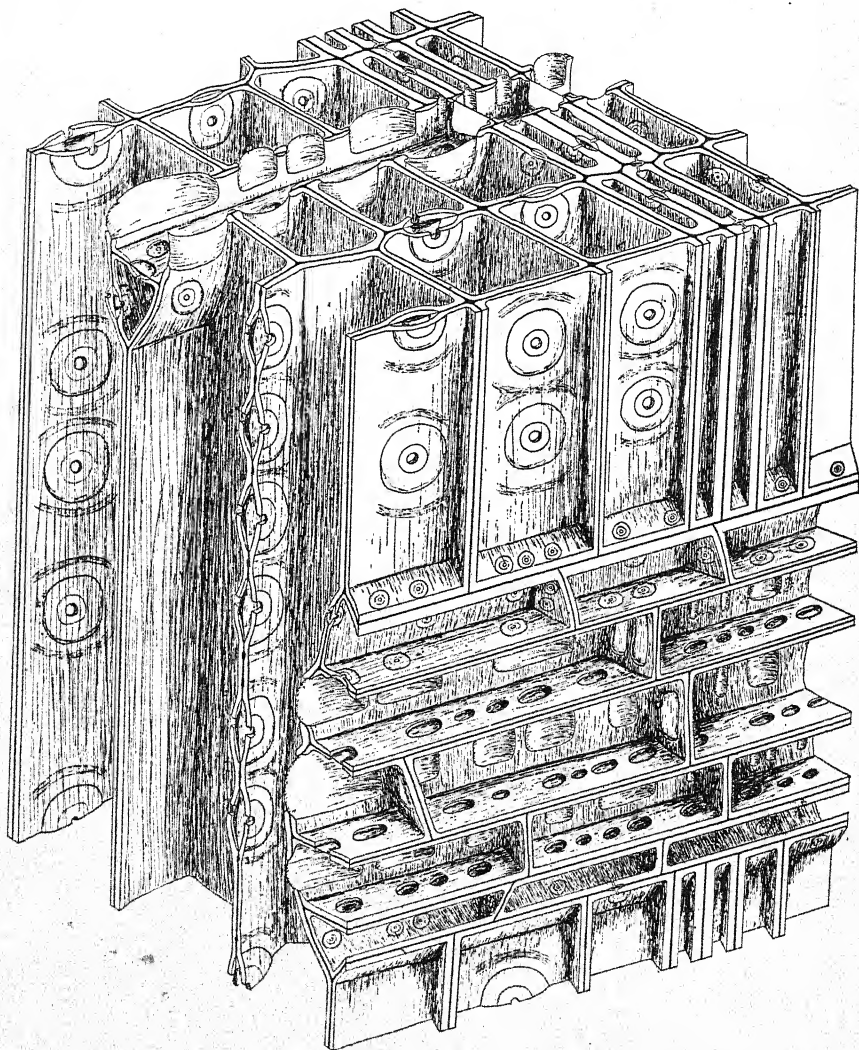


FIG. 86.—Secondary xylem of *Pinus Strobus*, showing details of structure. (The proportionate size of the ray is increased; only small parts of the tracheids are shown; the contents of the living ray cells are omitted.)

Picea and *Pinus* (except for that about resin canals). It is scarce in many other genera, such as *Larix* and *Tsuga*, where it is terminal. More abundant parenchyma, arranged diffusely, characterizes such genera

as *Juniperus*, *Thuja*, *Sequoia*, and *Podocarpus*. Vessels occur only in the Gnetales. Gymnosperm wood is thus very uniform in structure.

✓ **Structure of Angiosperm Wood.**—The wood of the angiosperms is characterized by the presence of vessels, and, in general, by a complexity of structure far greater than that of the gymnosperms. This complexity of structure is due to the presence of several kinds of cells—tracheids, vessels, fiber tracheids, fibers of various types, wood parenchyma cells (or some of these); to variety in ray form; and to the arrangement and interrelations of the different kinds of cells with one another. In most genera, vessels are abundant, and in some cases they constitute a considerable percentage of the wood, as in *Tilia* and *Populus* (Fig. 81). They are also abundant in vines and many herbs. In herbs with complete woody cylinders they are frequently less abundant, and are small. In roots, vessels normally make up a very large proportion of the wood. Only the wood of a few groups of angiosperms—the Trochodendraceae, some genera of the Magnoliaceae, and certain reduced, chiefly herbaceous forms—lacks vessels. Wood parenchyma is probably present in nearly all woody angiosperms, being abundant in some cases, as in *Carya* and *Platanus*, and scarce in others, as in *Acer* and *Liriodendron*. Typical wood parenchyma is absent in herbs with isolated vascular bundles and in some vines with bundles separated by wide parenchymatous rays. Fibers of several kinds may occur, even in a single species. Complexity and variety of structure are, indeed, prominent features of angiosperm wood structure; in this respect no tissue, unless it be angiosperm phloem, surpasses secondary xylem.

Xylem Rays.—The xylem ray partakes in the general function of the vascular ray, of which it constitutes the part inside the cambium. The vascular ray, from its structure and position, seems to serve for transverse intercommunication in the living parts of vascular tissue, and perhaps also, through accompanying, radially extended intercellular spaces, to some extent makes possible an interchange of gases with the outside atmosphere. By the agency of the vascular ray, water may be readily transferred from the xylem to the cambium and the phloem, and food supplies moved from the phloem to the cambium and to the wood parenchyma. In the latter cells and in the inner ray cells food for storage is readily passed inward from the phloem by the means of the rays. In the older, longer rays the terminal portions are not functional, the inner being included in heartwood, and the outer cut off, together with the surrounding cells, by periderm layers (Chap. IX).

The cells constituting a xylem ray are for the most part elongated in the direction of the long axis of the ray. They are typically prismatic, often distinctly rectangular, though the corners in many cases are rounded, and in very broad rays, as in *Quercus*, the cells may be round in cross section. Xylem rays vary in width, height, and longitudinal

extent. They may be one cell wide, as in *Pinus* (Fig. 86) and *Populus* (Fig. 81, A), when they are known as *uniseriate*; or two, *biseriate*; or several to many, *multiseriate*. Groups of closely placed, narrow rays, such as are found in *Alnus* and *Carpinus*, are called *aggregate rays*; and multiseriate rays of certain types are sometimes known as *compound rays*. The latter term is a poor one, however, since, in some cases at least, it is a misnomer. The cells of a xylem ray lie in definite horizontal rows, and the cells of contiguous rows are so placed that the ends of a cell do not coincide with the ends of the cells above or below. Neither do the end walls of the ray cells bear any relation to the walls of the cells of the vertical system. Structurally, the ray is more or less like a brick wall, the individual cells representing the bricks; the uniseriate ray is like a wall one layer thick; the biseriate, two layers thick, etc. In height, the rays range from one cell to very many, from a fraction of a millimeter to 8 or 10 centimeters. Rays only one or two rows of cells high are, however, not typical rays. Certain so-called "medullary rays" of vines and herbs may much exceed the maximum height given; these are, however, of different morphological nature. In a given species the rays may be of various width and height (Figs. 80, C; 83, C), or all may be of approximately the same width and the same height. For example, in nearly all gymnosperms the rays are uniseriate, but vary much in height (Fig. 79, C); in many species of *Quercus*, uniseriate and very large multiseriate rays occur (Fig. 82, A, C), no intermediate types being found, and the height of the rays varies. In *Betula* and *Acer*, the rays range from two to ten cells in width and are fairly constant in height; in species of *Diospyros*, the rays are alike in width and in height.

The shape of the cross section of the ray as seen in tangential sections of the wood varies greatly in different plants, being linear, oblong, fusiform, or round-fusiform. The type is usually constant for a species.

The length (radial extent) of a xylem ray is dependent upon the position of the point of origin of the ray in the xylem (for origin of rays, see Chap. VI). From that point the ray is continuous to the cambium; xylem rays are discontinuous between the point of origin and the cambium only in case of injury to the cambium. (It should be borne in mind that in any section false beginnings and endings of rays appear because the ray passes out of the plane of section and seems to end at this point.)

In most woods the rays are arranged without definite plan, except that of a fairly uniform distribution through the vascular tissue (Figs. 79, C; 83, C), such that in no case two rays come into contact, and no considerable areas exist between them. In certain woods, especially those of tropical genera, such as *Diospyros*, the rays occur more or less definitely in tiers. Aside from their position as radiating bands, rays bear in their arrangement no relation to the general stem structure; but the distribution of certain of the first-formed and of the very large rays

may be dependent upon phyllotaxy, these rays having a definite relation to the position of leaf traces.

Ray Tracheids.—The cells of the wood rays are usually all living, and of a type that differs from typical parenchyma chiefly in the presence of a thick, more or less lignified wall. However, in a few genera of the gymnosperms, for example, *Pinus*, the rays consist of both living and non-living cells. The latter are termed *ray tracheids* because they are tracheid-like in the lack of protoplasts and in the pitting and chemical nature of their walls, but resemble the living ray cells in their general shape and position in the ray (Fig. 86). In shape they are less uniform than the living cells, tending to be considerably longer, narrower, and lower. Ray tracheids occur normally at the upper and lower margins of the rays; hence they are often spoken of as *marginal ray tracheids*. The marginal rows of ray tracheids consist entirely of this type of cell; only very rarely here or elsewhere in the ray are two kinds of cells formed in one row. The number of rows of cells which may be of ray tracheids varies from one to several, one to three being most common. Rays consisting of only one, two, or three rows of cells may be entirely of ray tracheids; and where the rays are very high, there are often, near the middle of the ray, rows of *interspersed ray tracheids* in addition to the normal marginal rows. Ray tracheids, from their structure and position, apparently serve to conduct water radially.

Marginal Ray Cells of the Angiosperms.—Ray tracheids do not occur in the angiosperms. The rays of this group are not in all cases homogeneous, however. The wood of many genera, such as *Salix* and *Nyssa*, possesses rows of *marginal cells* different in size, shape, and contents from the other cells, and obviously different in function. Such cells are, however, always living cells. The longer diameter of these cells is vertical, or the cells are shorter than the typical ray cells. The pits of the lateral walls, especially those leading to vessels, are larger and more numerous than the corresponding pits of other ray cells. Marginal cells may form continuous rows, when they are said to be *conterminous*, or occur scattered along the marginal rows, when they are *interspersed*. The function of marginal cells in the angiosperms is not understood. In many woods these cells contain special secretions, such as essential oils, as in *Sassafras*.

Pitting of Xylem Cells.—The cells of the xylem ray are usually heavily pitted, both with each other and with the contiguous cells of the vertical system. The number, size, and type of the pits vary with the type of cells in the walls of which they lie (Chap. II). Thus, simple pits exist between living ray cells and other similar ray cells, and between such cells and wood parenchyma; bordered pits between ray tracheids and other ray tracheids, and between these cells and typical tracheids, fiber tracheids, and fibers; half-bordered pits between living ray cells and ray tracheids,

and between living ray cells and tracheids, vessels, fiber tracheids, and fibers. (It should be remembered that half-bordered pits when seen in face view often appear as full-bordered pits.) The pits between any type of cell and fiber tracheids and fibers are few and are reduced in size and structure as compared with pits between the more definitely conducting cells—tracheids, vessels, and parenchyma; in fibers of the extreme types, pit connection with many of the surrounding cells is often wanting.

The pits of gymnosperm wood as a whole are large; those of angiosperm wood very small, but much more numerous. The pits of gymnosperm tracheids and fiber tracheids are largely restricted to the radial walls of the cells (Fig. 86); in a few genera they occur also in the tangential walls, especially of the summer-wood cells, when they are known as *tangential pits*. In the angiosperms the pits are usually not restricted to particular walls; those of the radial walls, are, however, commonly more numerous. Pits in many cases completely cover a wall surface (Figs. 18, D; 19, B).

Bars of Sanio.—Horizontal, rod-like or band-like thickenings of the middle lamella in the walls of tracheids and vessels are commonly known as *bars of Sanio*. They are so named in honor of Sanio (Chap. XV), who first described them. These bars are pectic or cellulosic in nature, and are clearly seen, especially in many gymnosperms, when a strong cellulose-staining reagent is applied to the wood. By their presence the cell wall as a whole, however, is not increased in thickness, the secondary walls being proportionally thinner in those areas. Bars of Sanio lie between bordered pits, and in face view take the form of straight transverse rod-like bands, of similar structures with forked, curving ends, or of crescent-shaped bands (Figs. 16; 17; 86). When pits are far apart, two eyebrow-like bars or rims lie between each two pits; when pits are closer, the two bars between two pits fuse in the middle, the ends being free, "double rims" being formed. When the pits are crowded, the two curved bars become one straight bar. The curved bars of Sanio have been called *rims of Sanio*, the term "bar of Sanio" being restricted to the straight bands which appear, in some cases at least, to represent two rims of Sanio. This unfortunate confusion of terms is greatly increased by the fact that the term "bars of Sanio" is applied by some students to *trabeculae*.¹ These are structures of entirely different nature, being rod-like

¹ It is not clear that the term "bars of Sanio" should be applied to trabeculae on a basis of priority of usage, since trabeculae were first referred to as "Sanio's beams," and later as "Sanio's bands." It seems best, therefore, to continue the use of the term "bar of Sanio" as indicating any band-like thickening of the middle lamella related to pit position. The term "rim of Sanio" may then indicate the curved bar, if such a distinction is desirable. Apparently, these rims represent the thickened margins of the area between rounded "primordial pits" of the primary wall. When such pits are close together, the intervening wall space is reduced and the margins "unite."

projections of the cell wall lying across the lumen of tracheids (Fig. 23). Trabeculae occur as radial rods crossing in a straight line rows of tracheids formed by the same cambium cell. They are frequent in the conifers and have been found in the angiosperms. Bars of Sanio are conspicuous features of wall structure, but are not known to be of functional importance. Their presence is probably incident to the method of development of the primary wall.

Tyloses.—Balloon-like enlargements of cell walls, projecting into adjacent cell lumina through pit cavities, are known as *tyloses*. These

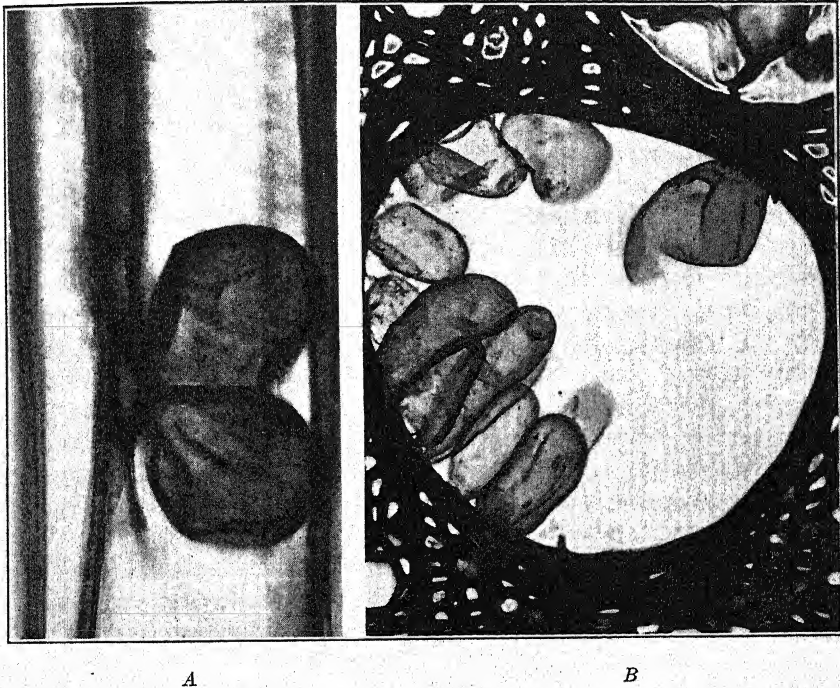


FIG. 87.—Tyloses. *A*, two mature tyloses, derived from pits in the same ray cell, in *Aesculus octandra*, $\times 680$. *B*, young tyloses in vessel of *Quercus lobata*. (After Gerry.)

structures are formed by the enlargement of the pit membranes of the half-bordered pits between wood parenchyma or wood ray cells, and vessels or tracheids. The delicate membrane is expanded, and grows, apparently by intussusception, pushing out of the pit cavity and protruding far into the lumen of the non-living cell (Fig. 87). A bladder-like extension of the parenchyma cell is thus formed, into which passes part of the cytoplasm and even the nucleus. After the tyloses are full-grown, starch, crystals, resin, and gum may be formed within them;

the presence of these substances in quantity is uncommon, however. The tylosis may remain small or become very large; its size and shape depend in part upon the size of the lumen of the tracheid or vessel into which it extends, and in part upon the number of other tyloses present. The wall of the tylosis may remain thin and delicate, becoming wrinkled and partially collapsed in heartwood, or may become thick and even lignified; pits may be formed in it when it comes in contact with other tyloses. The tyloses in a given cell may be few, as in *Populus* (Fig. 81, C), or many, as in the white oaks (Fig. 82), when they fill the lumen and become angular by compression. Tyloses are said to undergo division in some cases, "multicellular tissue," which fills the lumen compactly, being thus formed, as in *Robinia* and *Maclura*. That such division is responsible for the multicellular appearance, however, is questionable. The appearance of separate cells may be brought about by the presence of multitudes of tyloses, each slender, and all mutually compressed, as are soap bubbles in a crowded mass. Tyloses may develop from occasional pits only, as in *Juglans*, *Liriodendron*, and *Sassafras*, or from great numbers of pits, perhaps from every pit (leading to a living cell) in a vessel, as in *Robinia*, *Rhus*, and *Catalpa*. More than one tylosis may develop from a single parenchyma cell. Tyloses sometimes develop in the lumina of gymnosperm tracheids, as in the soft pines.

In the wood of conifers there is also found to some extent a closing of the cavity of resin canals due to enlargement of the epithelial cells (Fig. 84, C). These enlarged cells are often called tyloses, but are better termed tylosis-like cells. Other tylosis-like growths occur in protoxylem, where entire parenchyma cells or parts of cells protrude into the weakened or ruptured tracheid or vessel between the rings or turns of the spiral.

Tyloses are of common occurrence in angiosperm wood. They are characteristic of certain species, and always absent in others. Many tyloses develop about the time of transformation of sapwood into heartwood, but it is known that they may be present to some extent even in the outermost rings of sapwood. They are most abundant in heartwood, but may occur also in the sapwood whenever normally present in the heartwood. Tyloses also occur in the vessels of herbs. They have been described or reported in such genera as *Cucurbita*, *Coleus*, *Canna*, *Portulaca*, *Rumex*, *Asarum*, and *Convolvulus*. Not only do tyloses develop normally, but their formation may be induced in many plants by wounding. For example, they may develop in the region near wounds on the surface of a tree trunk or in the region where a branch has been removed; after the felling of a tree, tyloses may form in the sapwood throughout the log as it lies upon the ground. They may be present in the inner part of leaf traces after the leaf has fallen. Such tyloses, however, are usually sporadic in occurrence, and irregular in shape and size.

The development of tyloses either normally or as a result of wounding is said to be due to a difference in pressure in the cells on either side of a pit membrane; to the reduction of pressure; or to the cessation of conduction in the vessel, permitting the membrane to expand into the cell.

The distribution of tyloses in wood is not determined by type of wood, by rate of growth, by age of the plant, or by habitat. Where wood parenchyma is scarce, tyloses likewise are few; in such cases there is much variation in the frequency of their occurrence.

Tyloses are of considerable economic importance in the use of woods. They are a factor, though a minor one, in durability; durable species, with few exceptions, possess abundant tyloses—for example, *Maclura*, *Robinia*, *Juglans nigra*, *Morus*, *Catalpa*, and the white oaks. By blocking the vessel lumina they prevent rapid entrance of water, air, and fungal filaments. (Durability, however, is largely dependent upon the chemical nature of the wall.) The presence of tyloses prevents rapid penetration of artificial preservatives. For example, under treatment with creosote, red oak, which is without tyloses, is penetrated for long distances through the vessels, whereas white oak with tyloses is hardly penetrated at all. Similarly, white oak may be used in "tight" cooperage, whereas red oak with its open vessels is of little value for this purpose.

Sapwood and Heartwood.—Though little is known definitely about the conductive activity of xylem of different ages, it is probable that cells when first mature are most active, and that there is a gradual slowing down of conduction until functional activity ceases. So long as xylem contains living cells and is apparently conducting, at least to some extent, it is known as *sapwood*; after all activity ceases, it becomes *heartwood*. The terms *alburnum* and *duramen*, formerly much used for sapwood and heartwood respectively, are passing out of use. The sapwood of a tree serves for conduction, support, and food storage; the heartwood only for support. In the transformation of sapwood into heartwood a number of important changes occur: all living cells lose their protoplasts; the cell sap is withdrawn, and commonly the water content of the cell walls greatly reduced; any food materials present in the living cells are removed; tyloses, if characteristic of the wood, are formed; the partly lignified walls of parenchyma cells may become more strongly lignified; there are formed within or brought into the changing cells certain substances new to the tissue, such as oils, gums, resins, tanniferous compounds, various aromatic and coloring substances; flexible pit membranes become fixed in the closing position. In short, the xylem becomes physiologically functionless, being as heartwood merely a solid supporting column.

The extent to which the water content of the xylem is reduced with change to heartwood varies greatly: In a few plants—for example, *Ulmus* and *Pyrus Malus*—the heartwood remains "wet," that is, satu-

rated with water (whether such water is in process of conduction is doubtful, however); in other plants the heartwood may become very dry, as in *Fraxinus* (where in some species it is said even to become checked in the living tree). Such substances as oils, resins, and coloring materials may infiltrate the walls, and gums, resins, etc. may fill or partly fill the lumina of the cells. In *Diospyros* (ebony) and *Swietenia* (mahogany), the cell cavities are to a greater or less extent filled with a dark-colored, gummy substance. The color of heartwood, in general, is the result of the presence of these substances within the walls and, in some cases, the lumina. The fact that the heartwood is darker in color than the sapwood is incidental to the formation of these substances. Some woods, such as *Betula*, *Populus*, *Picea*, *Agathis*, have heartwood hardly if at all darker in color than the sapwood.

Heartwood, as timber, is more durable than sapwood, because the removal of water, the reduction of food materials available for fungi and bacteria by the disappearance of protoplasm and starch, the formation of such substances as resins, tannins, and oils, and the blocking of the vessel cavities by tyloses and gums render the wood less pervious to water and less subject to attack by the organisms of decay. For this reason, as well as for many others—such as the presence of desirable color or odor, or of substances of commercial value which may be removed, such as haematoxylin—heartwood is commonly of more value commercially than is sapwood. The latter, however, is preferred in some cases, as in some grades of quarter-sawed oak, and in hickory and ash for tool handles and spokes. Owing to lack of resin, gums, and coloring substances, sapwood is also preferred for pulp wood, and for wood to be impregnated with preservatives.

Apparently, there is no fixed length of functional life in xylem. The functional period is controlled by the physiological activity of the tree or of the organ or segment of the organ in question. Young, vigorous plants or vigorously growing parts of older plants have little or no heartwood, whereas slow-growing, weak, and most old trees have a very large proportion of heartwood in stem and root. In old trees the xylem remains sapwood but a very few years. In case vigorous growth is renewed, a large amount of sapwood is built up by the retention of all sapwood as such for many years. All parts of an annual ring are not changed into heartwood simultaneously; that is, the outer limit of heartwood bears no relation, necessarily, to the annual rings. Where strongly developed roots or branches are present on one side of a trunk, the xylem of the segment on that side remains alive long after other parts of the same age have become dead.

Relation of Microscopic Structure to Properties and Uses of Wood.—

The wood of different species varies greatly in its properties and in its value for different purposes. Characteristic qualities, and hence specific

economic uses, depend largely upon the histological structure and upon the chemical nature of the tissue. Variations in histological structure which affect the properties of wood consist chiefly in the kinds, proportion, and arrangement of cells—for example, the presence or the absence of fibers and of large vessels and their restricted or widespread distribution; the transverse diameter and the comparative thickness of the wall of fibers; the length of fibers and the extent to which they overlap other fibers; the straightness of fibers; the abundance and the width of the wood rays; the presence of tyloses. The amount and the distribution of wood parenchyma seem to bear little relation to the properties of wood. Variations in the chemical nature of the wood are of the greatest importance in relation to certain qualities of wood, especially those in which heartwood differs from sapwood. The cell wall itself varies in chemical nature, the proportions of cellulose, lignocellulose, and "lignin" differing greatly. Occasionally, the walls are even mucilaginous in nature. Tannin compounds may be present in considerable quantities as substances infiltrating the cell wall; the lumina may contain various amounts of gums, resins, tannins, etc.

Weight.—The wall substance of wood, either light or heavy, is of nearly the same specific gravity, about 1.56. Variations in weight are due to variations in the proportion of wall substance and of lumen space. Where the latter is small in amount, that is, where the wood is dense, it is, of course, heavy. Hence, abundance of small, thick-walled fibers makes a wood heavy as in *Guaiacum* (*lignum vitae*), *Diospyros* (Fig. 84, A), and *Pyrus* (Fig. 83); whereas numerous and thin-walled vessels, as in *Tilia* and *Populus* (Fig. 81), reduce the specific gravity greatly. Extremely light woods, such as those of the "cork-wood" type—for example, *Ochroma* (*balsa*) (Fig. 84, B)—have a very large proportion of large, empty, thin-walled parenchyma cells. The specific gravity of wood ranges from 0.2, as in *Ochroma* and *Leitneria*, to about 1.3, as in *Condulia*. The majority of well-known, commercially important woods range from 0.45 to 0.75 in specific gravity. Species of *Quercus* range in specific gravity from 0.65 to 0.95; *Carya*, 0.74 to 0.84; *Fraxinus*, 0.65 to 0.72; *Acer*, 0.62 to 0.69; *Pinus*, 0.37 to 0.79; *Abies*, 0.35 to 0.47; *Populus*, 0.36 to 0.41; *Sequoia*, 0.29 to 0.42; examples of heavy woods are *Guaiacum*, 1.1 to 1.4; *Eucalyptus*, 0.8 to 1.25; *Acacia*, 0.8 to 1.3.

Strength.—The presence of a large proportion of fibers or fiber tracheids makes a wood strong. Hence, dense and heavy woods are usually strong woods. The length of the fibers and the extent to which the ends overlap are apparently features of minor importance as regards the strength of the wood.

Durability.—Resistance to decay by the action of fungi and bacteria is dependent largely upon the chemical nature of the wood—of the cell walls and of the cell contents. It is not correlated to any degree (except

in some very light woods) with physical properties, such as weight and strength, or with structure. The presence of tyloses which block vessels does, of course, reduce the rapidity of entrance of fungal hyphae, and of water and oxygen. However, it is the presence or absence of infiltrating, natural preservative substances, such as tannin, resin, and oils, which determines the durability of wood. Both light and heavy woods are durable—for example, those of *Sequoia*, *Catalpa*, *Castanea*, *Robinia*, *Maclura*; and other equally light and heavy woods decay rapidly—for example, those of *Populus*, *Tilia*, *Acer*, and *Carya*. Resistance to decay is not necessarily correlated with depth of color, though heartwood is generally more durable than sapwood, and, in a general way, the darker the color the greater the resistance. This condition results from the fact that depth of color often indicates approximately the amount of preservative substances. Durability as resistance to mechanical destruction depends upon hardness, density, and toughness. Chemical resistance to decay is in such cases, of course, also of great importance.

Other Properties.—Flexible woods are fairly homogeneous and have long, straight, strongly overlapping fibers, and linear rays. This type of wood also cleaves readily. Toughness involves strength and pliability, and, to a large extent, the interlocking of the fibers. Thus, where the fibers are strongly interlocked, the woods may be put to special uses, that of *Ulmus*, for example, for hubs and basket splints; of *Ostrya*, for mallets and tool handles. The interlocking of the grain may be due in part, as in *Platanus*, to the presence of low, proportionately very broad rays around which the fibers bend in their course. Woods with interlocked fibers and of uneven texture are not readily “workable.” In all properties the proportion of water present is of much importance.

Penetrability by Preservatives.—The rate of penetration of wood by preservatives, such as creosote, is dependent to a large extent upon the structure of the wood. Such open channels as vessels and resin ducts provide ready access to infiltrating fluids, but the preservation of regions about these openings alone is of little value. Penetration through thick cell walls can occur only slowly. More rapid penetration through closed cells must take place through the pits, from lumen to lumen, as does the passage of water in living tissue. Passage through the pits undoubtedly is chiefly through the minute openings in the closing membranes (Fig. 16). Upon this movement the structure and the behavior of bordered pits have an important bearing. When living sapwood is immersed in a preservative fluid under pressure, that is, where pressure is from all sides, there is little or no penetration; when the preservative is applied at one end of a piece of wood with light pressure, penetration is fairly rapid, but with increased pressure it is quickly cut down. The cessation of penetration under the higher pressure appears to be due to the closure of the pits by movement of the tori (Figs. 15, C and 16, C). Practically,

green timber is not penetrable to preservatives. Such timber is sometimes treated under pressure in certain processes. In such cases, however, the preservative is not forced into the wood until the green timber has had the water boiled out in the treating retort, when it is, of course, seasoned timber. It is practicable to treat only seasoned timber with preservatives. The structural conditions responsible for the penetration of seasoned wood by preservatives are not well understood. It has been believed that microscopic checking of the cell walls is responsible for the passage of fluids from lumen to lumen, but such checking does not always occur, and the checking slits do not pass through the wall (Fig. 19, I, K). The pit membranes rupture only rarely in drying. It seems probable that the differences are due to changed conditions involving surface tension, capillarity, and the passage of fluids through very minute openings. In this case the openings involved are probably those in the closing membranes of the bordered pits. Although the lumina and pits are larger in spring wood than in summer wood, the latter is more freely penetrated by preservative fluids, whether the wood is green or dry. This is doubtless due to the fact that valve action of the closing membranes of pits in summer wood is very weak or lacking. Sapwood is always much more penetrable than heartwood. This is doubtless because in the heartwood the tori have become fixed in the lateral position, and the cavities of the pits are often clogged with gummy or resinous material. Even the lumina may be more or less filled by these substances or by tyloses.

Grain of Wood.—Variations in size, shape, and orientation of cells, and in proportion and arrangement of cell types, determine variations in appearance of wood, known as *grain*. Coarse grain, fine grain, and cross-grain are largely self-explanatory terms. Spiral grain refers to a condition in which the cells of the vertical system lie parallel with one another, but the whole system winds spirally about the tree. The grosser features of wood structure, annual rings and wood rays, form the most conspicuous grain of wood. The alternation of layers of coarser and finer cells, spring and summer wood, produce the prominent markings in many woods, such as the hard pines and the ashes. Wood rays when cut longitudinally, as in radial section, or obliquely longitudinally in sections that approach the radial, form conspicuous markings which are the more prominent because of the denser structure of rays and their tendency to take a high polish. Large rays, as in *Quercus*, form the *silver grain* of wood. The presence of silver grain, as in quarter-sawed oak, renders the wood of great value for furniture, cabinet work, etc. *Curly grain* is the result of an undulate course of the cells. This occurs in individual trees or parts of trees, and is frequent in *Betula*, *Castanea*, *Acer*, *Prunus*, etc. *Bird's-eye grain* is probably due to the presence of numerous dormant adventitious buds; these buds maintain their posi-

tion in the bark of the tree, building up weak central cylinders, chiefly parenchymatous, as the tree trunk increases in diameter. These pith-like steles form the "eye" when cut in cross section (tangential section of the wood), and the fibers and other cells of the vertical system swing around them as they do about the bases of branches.

Relation of Wood Structure to Climate.—Little definite information is available as to the correlation of wood structure and climate. The tropical woody flora is perhaps, as a whole, more primitive than that of the temperate regions, and hence may possess primitive characters in wood structure in a large proportion of species. Evidence on this point, though based on insufficient material, appears to be conflicting. Thus it has been suggested that scalariform vessels, uniseriate rays, and diffuse wood parenchyma, which are doubtless primitive characters, together with ring porous xylem, an advanced character, may be more common in temperate climate than in tropical climate plants. There can be no doubt, however, but that the gross structure of wood, especially those features which go to make up the grain as related to annual rings may be greatly affected by climate. Thus, alternate wet and dry, and warm and cold seasons favor the formation of sharply delimited annual rings, whereas in a uniform climate the yearly increments of wood are weakly or not at all set off from each other. Many tropical woods, both light and heavy, are very uniform in texture, owing to their homogeneous structure. On the other hand, some woods grown under the same conditions are not uniform in texture. Long growing seasons with high temperature and abundant moisture may favor the production of large amounts of wood substance, a condition which may be manifested by very rapid growth of relatively light, porous wood, or slower growth of wood with very dense structure. There are found in the tropics extremes of both of these types, as, for example, the remarkably light, rapidly growing wood of *Ochroma* (balsa) and the dense wood of *Diospyros* (ebony). Woody plants growing under severe climatic conditions, such as drought or cold, usually have wood of dense structure and small elements. In tracing such correlations it must be borne in mind that the factors influencing structure and growth are many and complex and that it is not always easy to determine causal relationships.

Compression Wood.—A type of wood somewhat darker than the sapwood, often reddish and resembling heartwood, is present in many gymnosperm genera, as in *Pseudotsuga* and *Pinus*. It occurs on the underside of branches, and on the lower side of tree trunks in trees that do not stand vertically. This wood is known as "redwood," or as *compression wood*, since it is always situated in regions where the weight of parts of the tree tend to compress it. Histologically, it differs only slightly from other wood, the cells being somewhat shorter and perhaps slightly thicker-walled.

Pith-ray Flecks.—Injury to the cambium region by insects known as “cambium-miners” produces ultimately areas of wound tissue in the mature xylem. These areas when seen in cross section appear as small patches of irregularly arranged, thick-walled parenchyma cells. They resemble wood rays (“medullary rays” or “pith rays”) in that they consist of parenchyma; hence they are commonly known as *pith-ray flecks* and as *medullary spots*. They have nothing to do, however, with rays or with the pith. These injuries are common in rosaceous woods, and also in the wood of *Salix*, *Acer*, *Betula*, and other genera. The insects causing the injury apparently belong to different groups, but are chiefly Diptera. The larvae bore along the branches and trunk, forming tunnels downward through the cambium or the immature xylem. The cavity thus formed is soon filled, however, by the proliferation of the surrounding cells. The cambium, if injured, is replaced, and growth is continued normally. Thus the strands of wound tissue are soon buried in normal wood. Such injury is of minor importance to the tree, but may greatly reduce the economic value of the wood, as in *Acer* and *Prunus*. (Pith-ray flecks are, unfortunately, sometimes explained as normal features of wood structure.)

Gummosis.—Another pathological condition, *gummosis*, deserves brief mention because of its frequent occurrence. As a result of injuries of various types which bring about exposure of tissue to slight drying, the cell walls become transformed into gum. The transformation appears to be the result of enzyme action, which first affects the pectic middle lamella and may ultimately dissolve the entire wall. Tissues affected by gummosis may thus be partly broken down, or become completely transformed into a mass of gum. The gum may be found filling the lumina of the affected cells, entering from the pits, or may be exuded from the tissue. Gummosis is common in woody plants, being extensive after insect and other injury in such plants as cherry, peach, and acacia. It perhaps occurs in the xylem of many plants as a response to injury or diseased conditions, and may incidentally protect tissues from further injury.

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CHAPTER VIII

SECONDARY PHLOEM

In the preceding chapter consideration is given to those secondary tissues formed by the cambium toward the inside of the stele and known as secondary xylem, or wood. The present chapter deals with the analogous tissues formed by the cambium toward the outside of the stele, designated by the term *secondary phloem*. The terms "inner bark" and "bast" have been used by various authors to indicate these tissues (Chap. IV), but, as these terms have also been employed loosely to indicate structures other than the phloem proper, their continued use leads only to confusion.

Extent and Amount of Secondary Phloem.—The extent and the amount of the secondary phloem depend upon the type of plant and upon the age of the part in question. The distribution of secondary phloem is, of course, controlled by that of the cambium. Hence, this tissue in its entirety may form a layer over all parts of the plant axis except the tips, and may extend outward upon the leaf and branch traces. In herbaceous stems where the vascular tissue is reduced and the stele broken, it may comprise, as seen in cross sections of the stele, only isolated groups of cells between the cambium and the pericycle. In such forms the tissue is radially thin, so that the total amount of such phloem is small. On the other hand, in a woody plant of considerable age, all the thick layer of tissue outside the cambium may be phloem, either living or dead, combined with variable amounts of periderm. Between these extremes are all gradations. Normally, the amount of secondary phloem is less than the amount of secondary xylem, both in the space occupied and in the number of cells formed. In woody plants this apparent difference in amount is exaggerated, not only because the older phloem becomes crushed, but also because the dead outer layers of phloem are actually lost either by weathering or by definite abscission.

✓ **Function of Secondary Phloem.**—The function of the secondary phloem is, in general, that already discussed in Chapter IV as belonging to phloem as a whole. Its special importance as a secondary tissue is that, in the majority of cases in the dicotyledons and the gymnosperms, it very soon replaces the primary phloem which becomes crushed and functionless. This is particularly true of the woody plants in which secondary thickening is initiated very close to the growing point and soon crowds out the delicate primary phloem tissue. In fact, in such plants,

the existence of the primary phloem is of such short duration as a functioning tissue that it is very difficult to study. It appears in sections of young twigs as obscure lines of crushed, thin-walled cells which have lost all semblance of their original form and structure. In some herbaceous dicotyledons this obliteration of the primary phloem is not so complete or, as in the potato plant, does not occur at all. In monocotyledons which have secondary thickening, the primary tissues remain intact. In general, however, it can be said that, in plants where secondary thickening takes place, the secondary phloem is the only phloem which is functionally important over any length of time. The development of this tissue from the cambium provides for its constant renewal, a very necessary feature since in most cases even secondary phloem is of short duration as functioning tissue.

Structure of Secondary Phloem.—Considered as a whole, secondary phloem is a complex tissue made up of a number of cell types, all of which have a common origin in the cambium. The arrangement and the proportion of cells of the different types vary greatly in different species. The elements which are normally present in all secondary phloem are the sieve tubes, which are accompanied by companion cells in the angiosperms; parenchyma of one or more types; and the phloem ray cells. Usually, some type of sclerenchyma is also present, and, less commonly, secretory cells, laticiferous ducts, or resin canals.

Sieve Tubes.—Sieve tubes (Fig. 37) are the most characteristic elements in all secondary phloem from the standpoint both of structure and of function. In some plants, such as the gymnosperms, they may make up the greater part of the phloem tissue, parenchyma and sclerenchyma occurring in smaller proportions. On the other hand, in most herbaceous plants, in seedlings, in young twigs of woody plants, and in the mature secondary phloem of such woody plants as *Carya cordiformis* (Fig. 88, D) and *Dirca palustris*, the proportion of sieve tubes may be much smaller than that of the other cell types. Sieve tubes also show great variety in arrangement. In the secondary phloem of some plants, such as *Liriodendron* (Fig. 89, A), *Juglans*, and *Tilia*, they may occur in more or less definite tangential rows or bands; in plants like *Carya*, they may be in somewhat isolated groups of three or four surrounded by other types of tissue (Fig. 88, D). In *Cephalanthus* (Fig. 88, C), the sieve tubes appear, in cross sections of the axis, in radial rows which are frequently interrupted by fibers, a condition not uncommon in shrubs which approach the herbaceous type. In fact, in woody plants almost any arrangement of sieve tubes with parenchyma and sclerenchyma may occur. In the secondary phloem of herbaceous plants generally, sieve tubes occur without definite regularity, although in certain groups, such as the Ranales, there may be a very symmetrical arrangement according to a definite plan.

The sieve tubes of the secondary phloem of dicotyledons are of many different types with respect to shape and to the nature of the end and side walls. In a given species the sieve-tube type is usually constant, except in juvenile stages, in the root and stem of seedlings, and in the growth of the first few years in twigs. In the gymnosperms the type is also uniform. Here the sieve-tube elements are not arranged in series, end to end, forming definite conducting lines, but are separate and distinct, in this respect resembling tracheids. Such sieve tubes have no definite end wall, the sieve plates occurring without regularity upon the radial walls (Fig. 90, A). In the angiosperms, however, great diversity of sieve-tube type is shown in the secondary phloem. In many woody species, such as *Carya cordiformis* (Fig. 90, B), the end walls of the sieve-tube elements are very oblique, frequently extending for nearly half the length of the element; in others, for example, *Pyrus* *Malus* (Fig. 37, M), end walls, as distinct from side walls, are obscure. Upon these oblique walls there are many sieve fields. At the other extreme of variation is the type found in *Robinia* (Fig. 90, C), *Maclura*, and in some species of *Ulmus* (Fig. 91, C) and *Fraxinus*, in which the terminal wall of the cell is transverse and made up of a single sieve plate. Between these types is a series of intergrading forms. No one type is predominant in the woody angiosperms; even closely related species, as those of *Fraxinus*, may have markedly different types. In the majority of cases the sieve-tube elements of the secondary phloem of herbaceous plants have transverse sieve plates; where oblique plates occur they are not of the extreme type found in the Juglandaceae.

The lateral walls of sieve-tube elements which abut upon other sieve tubes in secondary phloem are frequently covered with pronounced lattices (Fig. 37, H, S). These are well developed in some woody plants, such as *Ulmus* and *Populus* (Fig. 91, A), but are rare or wanting in other genera. The presence of well-marked lattices is not correlated with sieve-tube type as classified on the basis of the angle of the end wall; lattices may occur in any type. The sieve tubes of the secondary phloem of herbaceous plants are usually without prominent lattices.

Companion Cells. Companion cells (Fig. 37, H, I, S, T) are absent in gymnosperms, but are probably always present in greater or less abundance in angiosperms of all types. In some plants, such as *Juglans* and *Solanum*, they may accompany only a part of the sieve tubes; in others, for example, *Tilia*, there are from one to three companion cells with every sieve tube as seen in cross section. A companion cell may extend the entire length of the sieve-tube element to which it is adjacent; or, more commonly, at least in the woody plants, several shorter cells may extend along the sieve-tube element, the series occupying the full length of the element or only a part of it. Thus the number of companion cells accompanying a sieve-tube element ranges from none to several. Ordinarily,

✓companion cells can be most readily identified in transverse sections of the phloem by their appearance as small, triangular or rounded cells apparently located in the corners of the sieve tubes; the two cells together outlining the mother cell from which they have been derived. ✓In some cases companion cells may extend as narrow cells across the entire width of the sieve tube. In the secondary phloem of herbaceous plants, companion cells are supposedly present in all cases, though where the woody cylinder is well developed, as in *Lobelia* and *Solanum tuberosum*, they are frequently difficult to recognize because of the small size of all phloem elements in this type of plant. ✓In plants with less woody cylinders, such as *Cucurbita* and *Ranunculus*, the companion cells are of fair size and distinct. Companion cells show no great diversity of type, varying chiefly in length. ✓

Phloem Parenchyma. ✓Parenchyma cells are found in the secondary phloem of all plants, except in extreme herbaceous types where secondary phloem is small in amount, in some vines, and in woody forms of some genera and families which are predominantly herbaceous. The proportion of phloem parenchyma varies through wide limits. ✓In the gymnosperms, parenchyma cells are relatively few in comparison with the number of sieve tubes, a condition fairly constant in all species. In the angiosperms, however, there is great diversity. The secondary phloem of the seedlings and of the younger twigs of woody dicotyledons is largely composed of parenchyma, but in the more mature condition the proportion of these cells is much less. In some plants, as, for example, *Carya* and *Robinia*, there are few parenchyma cells in the secondary phloem of the older stems; in others, such as species of *Cornus*, parenchyma may predominate. ✓In herbaceous dicotyledons the proportion of phloem parenchyma is usually smaller—frequently much smaller—than that of the sieve tubes and companion cells. In many of the Compositae, however, the proportion of parenchyma is larger. In some families, such as the Ranunculaceae, and in certain genera in other families, no parenchyma is present, the phloem consisting wholly of sieve tubes and companion cells. ✓

The arrangement of the parenchyma in secondary phloem varies as does that of the sieve tubes. Thus, as seen in cross sections of phloem, parenchyma may occur in tangential bands alternating with bands of sieve tubes and fibers, as in *Liriodendron* (Fig. 89, A) and *Tilia*; in radial rows, as in *Cornus* and *Sambucus*; singly or in groups of a few cells, as in *Pinus*; or more or less definitely clustered about the sieve tubes, as in *Carya* (Fig. 88, D). In longitudinal section the cells are seen to form vertical series parallel with the sieve tubes (Figs. 89, B, C; 90, B, C, D).

The types of cells found in the parenchyma of secondary phloem show considerable diversity. This can be most readily understood by a consideration of the development of these elements from the cambium

(Chap. VI). Briefly stated, phloem parenchyma cells are formed directly from parenchyma mother cells, which, in turn, are formed from cambial cells. The cambial derivative may develop directly into a parenchyma cell, or, as is more commonly the case, divides transversely, forming two or more cells. Thus, phloem parenchyma cells may, as seen in longitudinal section, be elongated and pointed at both ends, resembling the cambial cell from which they were derived, or they may be rectangular or cylindrical, ranging from very elongate to nearly cubical or short cylindrical. The former, called *cambiform cells*, are not commonly found in the secondary phloem of woody plants, but rather in primary phloem generally, in herbaceous types, and especially in vines such as *Cucurbita*. Parenchyma cells formed by the transverse division of the parenchyma mother cell are common in the secondary phloem of all types of plants. Where the series of cells from a given cambial initial retains its identity (Fig. 90, C), members of such a series have been termed *divided cambiform cells* to distinguish them from those which have become so modified in shape that evidence of the origin of the series has been lost, and which are known under the general term, *conducting parenchyma*. Whatever may be the value of this distinction in primary tissues, these terms serve no useful purpose as applied to secondary phloem where distinct types do not exist. In such phloem there is an unbroken series of cell types from narrow, elongate cells formed without transverse division of the cambial derivative to short, almost cubical cells which have lost all semblance of relationship with the cambial initial. In the woody angiosperms two or more types of phloem parenchyma, distinct in form and function, are often found in the same tissue. In *Tilia americana*, for example, one type of parenchyma cell is elongate, heavily pitted, and usually associated with the sieve tubes; the other, short and broad, apparently without an active protoplast, and usually containing large crystals. ✓ In other woody plants, such as *Robinia*, the parenchyma cells are uniformly short and broad with thin walls and abundant pits. The secondary phloem parenchyma of herbaceous plants does not show the diversity of type shown in the woody plants. For the most part the cells are thin-walled and elongate, rectangular, or rounded, in cross section. ✓

Phloem Fibers and Stone Cells.—Sclerenchyma of one type or another is a characteristic feature of the secondary phloem of many plants. ✓ Fibers are very common and occur in a variety of form and arrangement. Frequently, they occur in definite tangential bands, as, for example, in *Liriodendron* (Fig. 89, A) and *Populus*. In other cases they are found singly, as in *Cephalanthus* (Fig. 88, C). In some woody plants which have a hard bark, as in *Carya* (Fig. 88, D), the fibers make up the greater part of the secondary phloem, and may more or less completely surround the groups of softer tissues. They provide, when abundant, considerable mechanical support for the stem. In *Dirca*, the twigs owe their tough-

ness largely to the phloem fibers. Fibers of secondary phloem were formerly used commercially to a considerable extent, and are still of some importance. The secondary phloem of various trees and shrubs of the Malvaceae, Tiliaceae, Moraceae, etc. has provided "bast" or "bast fibers" (Chap. IV) for economic purposes for centuries. The tapa cloth of the tropical Pacific Islands is composed chiefly of phloem fibers. ✓

In the gymnosperms are found all conditions from a complete lack of sclerenchyma, as in the phloem of *Pinus Strobus*, to well-developed tangential bands of fibers, as in *Juniperus*, and large masses of stone cells, as in *Tsuga*. In *Thuja occidentalis* the fibers are arranged in uniseriate tangential rows which alternate with rows of sieve tubes and parenchyma. Stone cells frequently occur in secondary phloem either alone or in combination with fibers. In some plants, for example, *Platanus* and *Fagus*, stone cells are the only type of sclerenchyma present in the phloem. In active phloem, stone cells are not generally so abundant as are fibers; but, as the phloem loses its power of conduction, the stone cells often increase in number. Thus, in the older, living, but probably non-conducting phloem of the woody plants, they may be abundant and present a great variety of form and arrangement. The occurrence of stone cells is further discussed in the consideration of the obliteration of the phloem.

Phloem Rays.—In vascular tissues formed by the cambium, rays are usually present. Only in reduced herbaceous types and in some specialized vines, such as *Clematis*, where secondary tissues are small in amount, are true vascular rays lacking. The diversity of type of vascular rays in secondary phloem is, naturally, as great as is that of the rays in secondary xylem; and the rays make up the same proportions of the tissue.

✓ Vascular rays are, of course, initiated in the cambium and extend into both the secondary xylem and the secondary phloem. Thus the phloem rays vary in width and height as do the xylem rays. They may be one cell wide, as in *Castanea* and *Salix* (Fig. 90, D); two or three cells wide, as in *Pyrus Malus*; or several to many cells wide, as in *Robinia* and *Liriodendron* (Fig. 89, D); or rays of various widths may exist in a species. ✓ In the oaks there are two types of ray, one very broad and the other uniseriate. Usually, the phloem rays are of uniform width throughout their extent. In some cases, however, they increase in width outwardly, the increase being due to the multiplication of the cells or to the increase in size of cells toward the outer end of the ray. This provides the necessary adjustment to the increase in circumferential extent of the phloem caused by the increase in the diameter of the axis. ✓ Phloem rays enlarging distally are especially prominent in twigs of certain genera, such as *Tilia*. ✓ The vertical extent of the ray in the phloem is as varied as its width, ranging from that of two or three cells, as in *Thuja*, to eight to ten centimeters, as in the broad rays of the oaks. Rays consisting of a single row of cells occasionally occur. Marginal cells, different in

type from the other ray cells, but parenchymatous, are sometimes found, as in *Salix*.

The abundance of rays is, in part, dependent upon their size. Broad rays are spaced farther apart than are those of the narrow type. In woody plants that approach the herbaceous habit, as, for example, *Cephalanthus*, the rays as seen in transverse section of the phloem (Fig. 88, C) are separated by only one or two rows of sieve tubes or parenchyma. With the exception of the large rays found in some families, herbaceous plants are characterized by uniseriate rays occurring at frequent intervals. In herbs with reduced vascular tissue the vascular rays have in their evolutionary development been reduced, and in some forms have disappeared.

Phloem ray cells are for the most part of uniform type. In woody plants, the common form, as seen in cross section, is rectangular and radially elongated. In semi-herbaceous and herbaceous plants the cells tend to become cubical or globose. Transitional forms are frequently seen in shrubs, such as *Cephalanthus*, and in "woody" herbs, such as *Agri-
monia* and *Potentilla*. In such cases phloem ray cells closely resemble phloem parenchyma and can only be distinguished from the latter by a study of the series of cells back to the cambium and to the rays of the xylem. All phloem ray cells are of the parenchymatous type with active protoplasts. In age, many of them may become stone cells. A special type, of much importance, is the so-called *albuminous cell*, or marginal ray cell, of the gymnosperms. These albuminous cells are situated at the upper and lower margins of the phloem rays and differ from the ordinary ray cells functionally. Apparently they are intimately connected in function with the sieve tubes. One of the most evident differences between the albuminous cells and the ordinary phloem ray cells is that the former do not contain starch. Structurally, these albuminous cells differ in that they are joined directly with the sieve tubes by sieve fields, and, further, are of greater vertical diameter than are the normal ray cells. These cells are closely related to the sieve tubes in their development and retain their protoplasts only as long as the sieve tube is functioning. Callus pads form within the albuminous cells over the sieve-plate-like connections with sieve tubes at the same time as the development of callus occurs in the sieve tubes themselves. Albuminous cells are in a way comparable with the marginal ray tracheids of the xylem. Cells suggestive of albuminous cells in appearance and position are found in the phloem rays of some woody dicotyledons, such as *Nyssa* and *Cornus*; these are not, however, the functional equivalents of such cells. In the gymnosperms the albuminous cells have been said to function much as do companion cells in the angiosperms.

From the standpoint of function, the secondary phloem is a complex tissue system with most of its parts interrelated in a definite manner.

Thus, the sieve tubes, companion cells, and some parenchyma cells are structurally adapted to vertical conduction, whereas the phloem rays provide a means of horizontal conduction to and from the xylem and cambium. Sieve tubes are ordinarily pitted heavily only with other sieve tubes and with companion cells, or in the gymnosperms, with the albuminous cells. The parenchyma cells which are given over to crystal storage lie usually close to fibers, where they may form extensive rows and even completely ensheath the strands of fibers. The different types of parenchyma concerned with conduction frequently lie adjacent to the sieve tubes from which they are separated only by a thin wall. These parenchyma cells are not, however, conspicuously pitted with the sieve tubes nor with the companion cells, although they are usually heavily pitted with each other upon both their radial and their transverse walls. In some woody plants, for example, *Castanea* and *Cornus*, the pits in these cells are clustered in a way that strongly suggests sieve plates (Fig. 91, D). Phloem ray cells are frequently pitted with conducting parenchyma of this type. Taken as a whole, phloem has to do with the conduction of elaborated food products, both protein and carbohydrate, and possibly with mineral nutrients as well. Just which substances, however, move in the sieve tubes and which in the parenchyma is not known. From the fact that the proportions of conducting parenchyma tissue to sieve tubes show such great variation, and that the latter are almost or quite lacking in some cases, as in slender vascular bundles and in primary phloem of woody plants, it may be inferred that parenchyma under some conditions may perhaps perform the functions of sieve tubes, or that the functions of the two types of cells may be interchangeable.

Another important function of phloem parenchyma is the storage of starch and possibly of other organic materials. Such storage occurs usually in cells especially adapted to the function, and not in the heavily pitted parenchyma cells that serve for conduction. Storage parenchyma cells are usually of rather large diameter with inconspicuous pits. Phloem ray cells are often packed with starch during the dormant season. This is especially true in roots where the phloem rays may be relatively large. The comparative absence of sclerenchyma in roots gives more space for the abundant storage parenchyma. Specialized parenchyma cells containing various secretions occur abundantly in some secondary phloem, both in the vertical system and in the rays.

As has been previously stated, the secondary phloem tissues are frequently arranged in definite tangential bands. Such layers of tissue often have the appearance of annual rings. However, these ring-like bands do not have definite seasonal limits as do those of the secondary xylem, because there is no distinction between the phloem cells formed in the early spring and those of the late summer comparable to the difference between spring wood and summer wood. Further, the last xylem

cells formed in a season from the cambium become fully mature and lignified before growth ceases. On the phloem side of the cambium, on the other hand, at the end of the growing season there are usually several rows of cells that have not completely differentiated, but which remain dormant until growth is renewed, when they mature to form normal sieve tubes. Therefore, there is no clear difference between the phloem cells formed in two consecutive seasons. There may exist a seasonal formation of sclerenchyma bands, but it is not known that there is any constancy in such growth. In fact, the number and the width of these bands of sclerenchyma is apparently dependent upon environmental factors and vigor of growth. In tropical plants, new layers of phloem as well as of xylem are formed with each "flush" or period of new growth; these have, of course, no distinctness as layers comparable with the annual rings of temperate-zone plants.

Cessation of Function of the Phloem.—The length of the functioning life of the secondary phloem, at least that of the sieve tubes and companion cells, is brief as compared with that of secondary xylem. In some woody plants the sieve tubes may function for a single season only, and in some tropical trees for a single "flush" of growth. In other species, and frequently in roots, these cells may be active over a longer period, even up to several years. The phloem parenchyma and the phloem ray cells—other than the marginal albuminous cells of the gymnosperms—commonly remain alive and apparently in normal condition long after the sieve tubes have lost their protoplasts. The cessation of activity of the entire tissue appears to be gradual, becoming complete only when periderm layers have formed within it, depriving all cells of food and water supply from the tissues beneath.

The exact time of loss of function by the sieve tubes is in doubt. It is generally believed that these cells function from the time of disappearance of the nucleus until the protoplast is lost. Recently the opinion has been expressed that the functional life of the sieve tube ends with the disintegration of the nucleus. The fact that this is the actual condition does not seem to have been established, however.

Closely tied up with the functioning life of the sieve tube is the formation of the callus pads over the sieve plates. In many cases these are deposited at the end of the growing season, thus occluding the sieve tube while the plant is dormant; with the resumption of growth in the spring, the pads are dissolved and the sieve tubes again become functional. In other cases, however, the plugging of the sieve pores with callus marks the permanent cessation of function of the cell.

The disappearance of the protoplasts of the sieve tubes and companion cells certainly indicates loss of function in these cells. This in many cases, as, for example, in *Robinia*, *Quercus*, and *Pyrus*, is accompanied by, or followed sooner or later by, the crushing and radial flattening of

the sieve tubes. This cell destruction is caused by the pressure of the growing tissues beneath upon delicate, dead cells. The collapse of the sieve tubes may be so complete that a group or layer of such crushed cells is represented only by an irregular band of structureless wall substance. In some cases even this may be removed by absorption. The crushing of the sieve tubes is sometimes spoken of as the *obliteration* of these cells. In many plants, such as *Pinus Strobus*, *Robinia Pseudo-Acacia*, and *Clematis virginiana*, sections of phloem in the dormant condition show only a narrow band of tissue with the sieve tubes intact, or even no mature uncrushed sieve tubes (Fig. 91, B). Outside of this region the sieve tubes are crushed and functionless. In other plants, such as *Tilia* and *Populus*, the sieve tubes may not be crushed for a considerable distance from the cambium, but all those not close to the growing region have lost their contents, and thus apparently have ceased to function. In other plants, for example, *Salix*, the sieve tubes are not crushed at any time, remaining normal in size and shape even after the formation of periderm layers which cut them off from the living tissues beneath. It is doubtful, however, if the sieve tubes in any case become lignified as the phloem grows old as do many of the surrounding parenchyma cells.

The changes which take place in phloem as it ages show great diversity in minor details in different species, but, in general, involve approximately the same phenomena. Simultaneously with, or following, the death of the sieve tubes, lignification of many or all phloem parenchyma and ray cells may occur. Druses and other crystals are formed in great number, both in parenchyma and in the newly formed sclerenchyma. In many plants the crystals form in thin-walled parenchyma, which lies beside and often ensheathes the fibers (Fig. 8, K-N). Additional gums, tannin, and resins may be deposited in the parenchyma at this time. In annual herbaceous stems the phloem probably remains functional throughout the life of the stem, or at least until the maturation of the seed. Few changes occur in such tissue, although in certain Compositae the phloem parenchyma becomes lignified toward the end of the growing season.

The manner and the extent of sclerification in the outer secondary phloem are varied. In such woody plants as *Fagus* and *Platanus*, nearly all cells, with the exception of sieve tubes and companion cells, become transformed into stone cells, and the bark is, consequently, very hard but not tough. Fibers in these cases may be wanting. Many trees, for example, *Quercus*, show a mixture of stone cells and fibers in old secondary phloem. Phloem rays frequently become lignified at their outer ends, that is, as the cells become old. In the oak the cells of the broad phloem rays become lignified when still young and close to the cambium. In *Salix* and *Juglans*, and in many other genera, no stone cells are formed, the outer phloem consisting largely of fibers.

Not always is additional sclerenchyma formed as phloem ages; the increase in the proportion of sclerenchyma in the outer phloem of some species is only apparent, and is due to the collapse of the softer tissues, rather than to the lignification of additional cells.

The economic uses of the secondary phloem as a source of fibers have already been mentioned. Other uses are as a source of tannin, as in the case of oak, chestnut, and hemlock bark, and along with the cortex, of some spices and drugs, for example, cinnamon and quinine. Secretory canals are often abundant in phloem, and the secretions may be of much economic value, as in the case of rubber, which is obtained from the latex of *Hevea* and other genera; and various resins, such as Kauri gum, obtained from *Agathis*, and spruce gum, from *Picea*.

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CHAPTER IX

PERIDERM AND ABSCISSION

In all plants which have secondary growth there is an adjustment on the part of the epidermis and cortical tissues to the resulting increase in diameter; or, in case the outer tissues are ruptured, some provision is made for the protection of the underlying tissues from desiccation. In herbaceous types generally, and in some woody plants, this adjustment is accomplished by the proliferation and increase in size of the cortical and epidermal cells. These cells in herbaceous plants often do not lose their capacity for division until the axis has attained approximately mature size, and in woody plants cell division in these outer primary regions may continue even after the first year. The comparatively short life of herbaceous axes also makes it possible for the outer layers to endure the effects of weathering without the renewal of the exposed protective tissues. In the majority of woody plants, on the other hand, the increase in diameter of the axis is so great that there is usually some special provision for the protection of the inner tissues as the increase in diameter takes place. During the early life of the axis, the epidermis may increase in circumference by division and expansion of the cells sufficiently to accommodate the increase in diameter. In at least a few woody plants, as, for example, *Acer pennsylvanicum*, *A. Negundo*, *Menispermum canadense*, and species of *Cornus* and *Viburnum*, the epidermal cells continue to divide slowly at least into the second year. In such cells the cytoplasm is more abundant and the nuclei are proportionately much larger than in typical epidermal cells. In most species, however, the functional duration of the epidermis is but a short time, extending over only a few weeks or months. When the epidermis ceases to function, a new protective layer, known as *periderm*, is formed.

Structure of the Periderm.—The periderm commonly consists of three layers of tissue: the initiating layer or meristem, known as the *phellogen*, or *cork cambium*; the layer of cells formed by this meristem toward the outside, the *phellem*, or *cork*; and usually a layer formed toward the inside, the *phellogen* (Fig. 92).

Phellogen.—The phellogen is an excellent example of a secondary meristem in that it arises from living cells that have become permanent. It is a lateral meristem, in that it increases the diameter of the axis, cutting off cells on the tangential faces for the most part in much the same way as does the true cambium. In shape, the phellogen cells show little

variation. As seen in tangential section, they appear polygonal and more or less isodiametric, except in a few special cases; in transverse

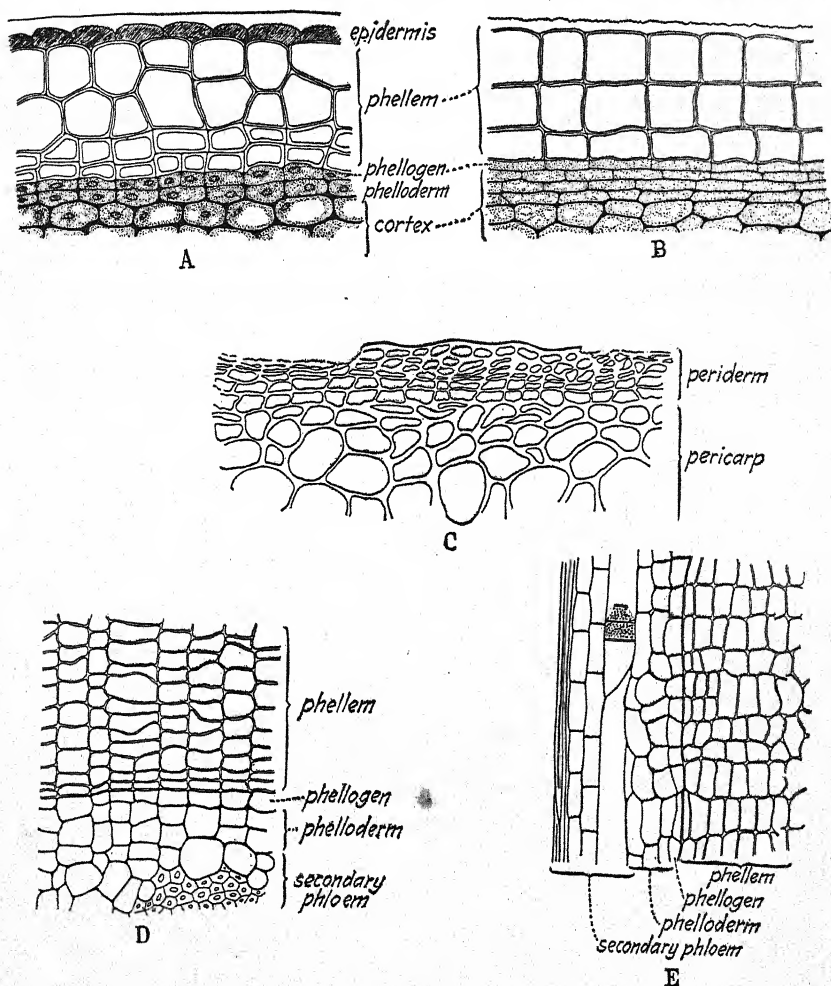


FIG. 92.—Periderm. A, B, C, cross sections of superficial layer; D, E, cross and radial sections of a deep layer. A, in twig of *Populus deltoides*. The phellogen arose in the outermost cortical cells, and has formed four layers of phellem cells and one of phelloderm; the phellem is capped by the dead, tannin-filled epidermis cells. B, in twig of *Solanum Dulcamara*. The phellogen arose in the epidermis, the outer halves of the epidermal cells have become typical phellem cells; they are capped by the cuticle. No phelloderm has been formed. C, in fruit of *Pyrus Malus*. The outer cells are readily loosened, the periderm becoming "scurfy." D, E, in secondary phloem of *Salix alba*, var. *vitellina*. The phelloderm cells are somewhat irregularly arranged.

section they appear rectangular and radially flattened. Except in the lenticels, intercellular spaces are lacking.

In the formation of a phellogen layer, mature living cells become meristematic and form a continuous uniseriate layer of initials. This always

occurs in epidermal, cortical, or other tissue where living cells are sufficiently abundant to permit the formation of a layer of considerable vertical and tangential extent. When the formation of a phellogen is about to take place in epidermal cells, the protoplasts lose their central vacuoles and the cytoplasm increases in amount and becomes more richly granular. After the formation of this initial layer, tangential, and, to a lesser extent, radial division takes place, much in the same manner as does division in the true cambium. The derivative cells are normally arranged in radial rows, the cells of the phelloderm being less markedly so than those of the phellem. In periderm, the number of tangential rows of undifferentiated cells present at any one time during the period of activity of the phellogen is usually much less than the number of similar rows in the cambium zone during the growth period of the cambium. In fact, in periderm the only immature cells to be found are frequently the row of initials, the cells formed by this meristem having all matured before further division of the phellogen.

In the ratio of the number of cork cells to phelloderm cells formed by the phellogen, considerable diversity is shown in different plants. Generally, several to many times as many cells are cut off toward the outside (phellem) as toward the inside (phelloderm). In some cases, indeed, phelloderm may be practically absent; more rarely, it may be even greater in amount than the phellem. In the cork oak, *Quercus suber*, and in plants with corky-winged stems, such as species of *Euonymus*, *Liquidambar*, and *Ulmus*, the phellogen forms great numbers of soft cork cells and relatively very little phelloderm.

Phellem.—The cells constituting phellem, commonly known as cork cells, are for the most part uniform in shape, in this respect like the cork cambium cells from which they were cut off, namely, polygonal, as seen in tangential section, and often radially thin as seen in transverse sections of the stem (Fig. 93). In the maturing of phellogen derivatives there is no gliding growth or complicated differentiation comparable with that which occurs in the formation of vascular tissues. In shape, the cells of some types of thin-walled cork may be radially elongated, as in commercial cork (Fig. 93, A, B); in the superficial persistent periderm of plants like *Betula* and *Prunus*, the cork cells are conspicuously elongated tangentially (Fig. 93, D, F). Cork cells are tightly fitted together and lack intercellular spaces.

The cell walls of cork cells are characteristically made up of three layers: the middle lamella, which may be either of cellulose or lignified; laid upon this, a suberized layer, or *suberin lamella*; and, next the lumen, a cellulose layer, which in some cases may be lignified. In thin-walled cork the inner, cellulose layer is absent. Often the various layers are not readily seen. The substance suberin, which is believed to make up the suberin lamella, is similar in its properties to cutin, in that both are

highly impervious to gases and water, are highly refractive as seen under the microscope, and resist the action of acids. Cork tissue in some few species—notably, *Quercus suber*—is elastic to a high degree, this quality

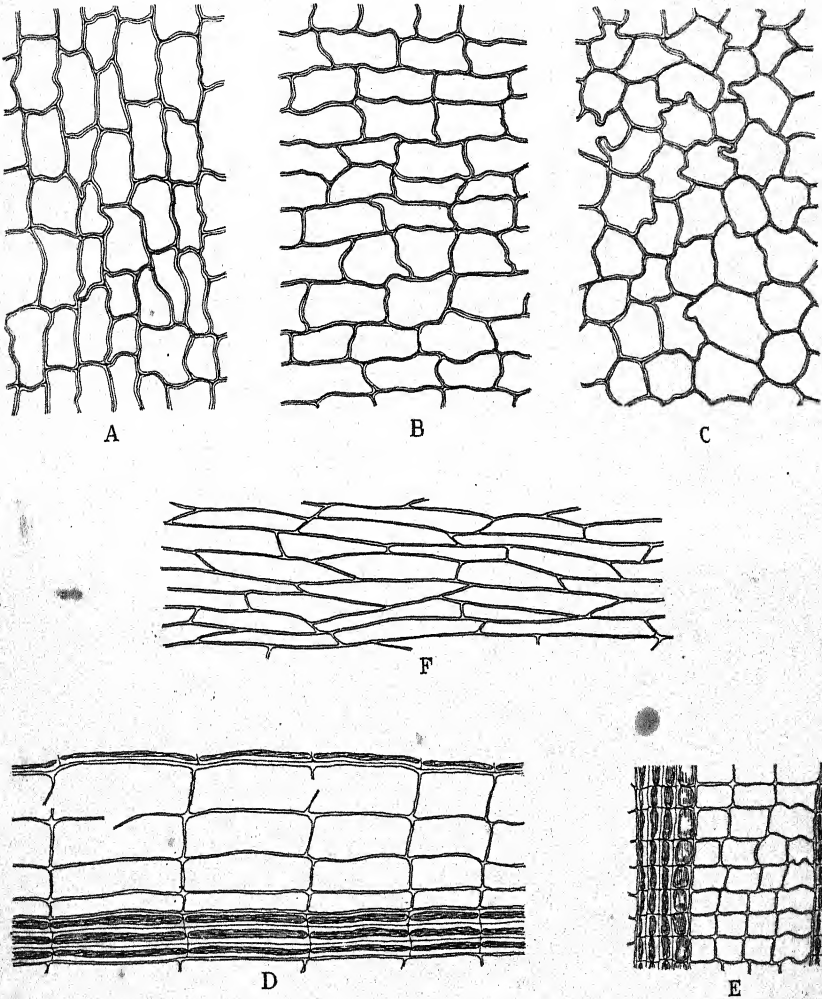


FIG. 93.—Phellem. A, B, C, commercial cork, from *Quercus suber*, transverse, radial, and tangential sections respectively. D, E, F, birch "bark," from *Betula alba*, transverse, radial, and tangential sections respectively. D and E show a complete (probably annual) layer, of two kinds of cells, the larger, thinner cells showing the tendency to rupture which causes birch "bark" to peel in thin, papery sheets.

depending in part upon the elasticity of the cell walls themselves, and in part upon a change in the shape of the cells as the stretching takes place; in the majority of plants, however, the cork tissue formed is both inextensible and inelastic. It is to the nature of cork cells—the suberized

walls and compact arrangement—that periderm layers owe their functional value in the prevention of water loss.

A number of different types of cork cells occur. Of the two common types, one is thin-walled, empty, and radially elongate, making up the light tissue of the bottle-cork type; the other is thick-walled, and radially flattened, with the lumen filled with dark-staining material of a resinous or tanniferous nature. These two types may be found separately in different plants or in alternating bands in the same plant, as, for example, in *Betula* (Fig. 93, *D*, *E*). In such a case the resulting “bark” is stratified and separable into thin, paper-like sheets. In rare cases stone cells and cells with crystals are formed in the phellem.

Mature cork cells are non-living and usually without pits. Where pits have been reported, they are described as through the inner cellulose layer (that next the lumen) only, a condition possibly conducive to the translocation of materials in the formation of the suberin lamella.

Phelloderm.—The cells of the phelloderm are living cells which are more or less loosely arranged, and which in most cases do not differ from adjacent cortical cells except in that they are arranged more or less definitely in radial rows. In some cases they function in photosynthesis and in starch storage. They are normally pitted with each other through their cellulose walls as is the case with other parenchyma. Stone cells and other specialized cells occasionally occur in phelloderm. The term “secondary cortex” is sometimes applied to phelloderm. It is, however, more frequently applied to periderm as a whole, this layer being a “cortex” in the physiological sense of protection. Since the periderm often develops secondarily in phloem, however, the term “cortex” cannot logically be applied to it. The use of the term “secondary cortex” in either sense is clearly undesirable.

Duration of Periderm.—In the majority of woody plants any given phellogen layer functions only for a brief period of time; its component cells then mature to form cork cells. In periderm layers of this type there is no seasonal regularity of activity. On the other hand, in certain species with persistent, superficial periderm layers, as, for example, species of *Betula*, *Prunus* (Fig. 98), and the cork oak, *Quercus suber*, there is seasonal activity of the cork cambium with the resultant formation of rather conspicuous bands or layers of cork which probably represent “annual rings” (Fig. 94, *B*). This condition is readily visible in bottle cork, where the rings resemble the annual rings of xylem. In *Betula* also the layering is prominent (Fig. 93, *D*, *E*). It is because of this alternate formation of thick-walled and thin-walled cells and the ease of rupture of the latter, that birch periderm splits into thin, papery sheets.

Commercial Cork.—The development of the periderm layers in the cork oak, *Quercus suber*, represents a case of special interest. Here the phellogen first arises in the epidermis, forming externally masses of cork

tissue and internally relatively few phelloderm cells. This phellogen persists indefinitely. At the age of about twenty years, when the tree is about 40 centimeters in circumference, this outer layer, known as virgin cork, is removed by stripping, the break being made probably through the phellogen layer, though possibly through the phelloderm. The underlying exposed phelloderm and cortical cells die, and a new phellogen layer is formed several millimeters deeper in the cortex. By this phellogen new cork is formed more rapidly than the first layer, and after nine or ten years the new cork layer has attained sufficient thickness to be commercially valuable and is again removed. This cork is of better quality than the nearly useless virgin cork, but is not so good as the third and

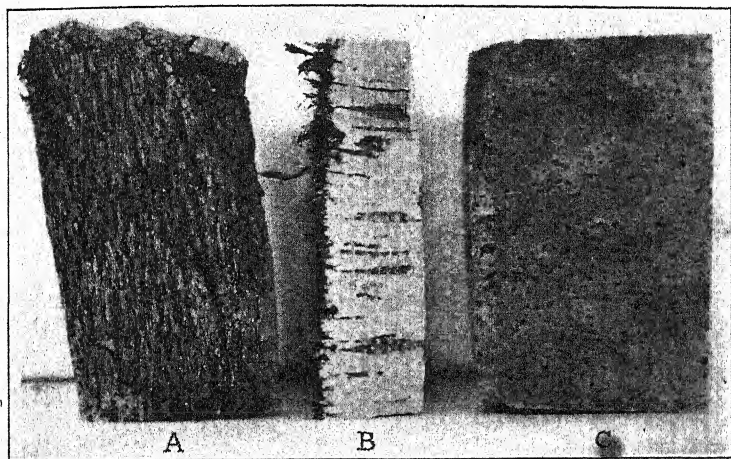


FIG. 94.—Phellem of *Quercus suber*, commercial cork as it comes from the tree. A, the weathered outer surface, showing fibers and rays of the secondary phloem, tissues cut off and killed by the formation of the underlying phellem. B, cross section, showing "annual rings," and lenticels in longitudinal section, the torn phloem fibers of the outer surface on the left. C, the smooth inner surface, along which the layer was peeled from the trunk, showing cross sections of the lenticels.

subsequent strippings which take place at intervals of about nine years until the tree is 150 or more years old. After the successive strippings the new phellogen layers develop at greater and greater depth in the living tissue. Hence the cortex is lost in the first few strippings and the subsequent cork layers form in the secondary phloem. A strip of "cork bark," therefore, has one smooth surface, the inner, where the phellogen was split (Fig. 94, C), and one rough surface which has been cracked by weathering. Upon the rough surface there is apparent the remains of the secondary phloem which was killed by exposure after the stripping of the previous layer (Fig. 94, A). If the trees are not stripped, the initial periderm layer probably persists indefinitely, forming cork of

considerable thickness. The cross section (Fig. 94, B) shows the bands which are probably annual layers.

Extent of the Periderm.—Considered in its entirety, any given phellogen layer extends as a sheet of tissue more or less parallel with the circumference of the axis. The longitudinal and circumferential extent of a layer varies greatly, and is dependent upon the species concerned and upon the age of the axis. In twigs, the first layer forms a continuous cylinder. In stems the extent of later formed layers is only rarely as great, and usually it is much less. In a few cases, as, for example, in *Fagus grandifolia*, there may be a persistent superficial layer of periderm over the entire trunk and branches up to near the growing points. The periderm layer of roots is commonly a continuous layer covering the entire surface except the growing tips. In most stems, however, any given sheet of cork cambium (after the first) covers only a small part of the surface of the axis. Sometimes these layers may be only a few square centimeters in area, but in others their extent is much greater. The periderm layers formed at different times either overlap or join each other so that together they form a continuous corky covering over the stem (Fig. 96).

✓ **Origin of the Periderm.**—The origin of the first phellogen layer to be formed on the young stem is always in mature living cells in the tissues outside the phloem. In many species, for example, *Pyrus Malus*, *Viburnum Lantana*, and *Solanum Dulcamara* (Fig. 92, B), the first layer of cork cambium is differentiated in the epidermis itself. It is of more common occurrence, however, for the phellogen layer to be formed in the layer of cells just beneath the epidermis, as in *Populus* (Fig. 92, A), *Magnolia* (Fig. 92), *Castanea*, *Ulmus*, and *Juglans*. In such cases the epidermis is soon broken and disintegrated. In the potato tuber a phellogen arises both in the epidermis and in the subepidermal layer (Fig. 95); however the outer meristem does not function. More rarely the first-formed cork cambium of stems has its origin deeper in the cortical tissues, or even in the pericycle, as in *Ribes* and *Thuja*. In such cases the outer tissues, being deprived of food and water, soon die and are sloughed off. In roots deep periderm formation is characteristic, the phellogen forming just beneath the endodermis and persisting as a continuous layer over the entire root system except near the tips.

The length of time over which the first-formed periderm layers persist as functioning tissue varies greatly in the different woody plants. In a considerable number of cases—for example, *Fagus*, *Carpinus*, and *Betula*—the original periderm may persist for a great many years or for the life of the tree. In these cases the increase in circumference is accomplished by the radial division and subsequent enlargement of the phellogen cells. In the majority of plants, however, the first-formed periderm layer on the stem is replaced sooner or later by other periderm

layers which arise successively deeper and deeper in the cortical, and ultimately in the phloem tissues (Fig. 96). In some cases these internal periderm layers form continuous sheets of tissue parallel with the outer layer, and concentric cylinders of cork result. Such a condition is found

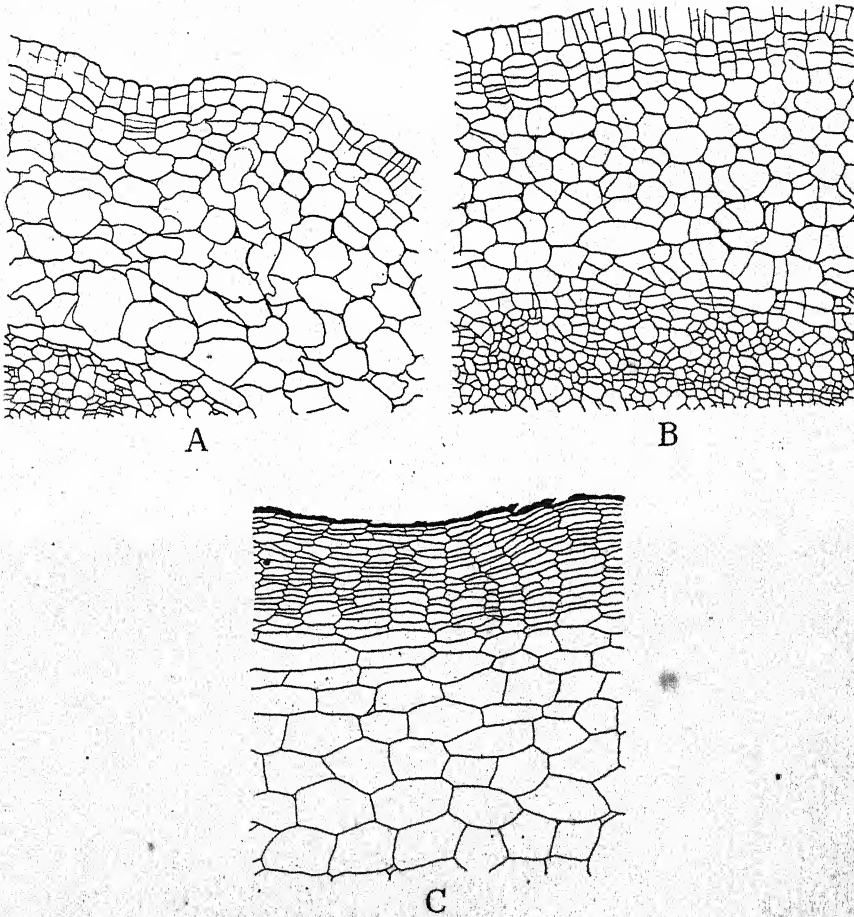


FIG. 95.—Periderm in the potato tuber (var. Irish cobbler). A, B, cross sections of outer part of young tuber, showing origin of periderm: A, two phellogen layers arising, one in the epidermis, one in the subepidermal layer; B, the inner phellogen dividing, the outer not developing. A and B, $\times 100$. C, cross section of outer part of mature tuber showing thick phellem. C, $\times 40$. (After Artschwager.)

in *Vitis*, where the outer cylinders are broken and sloughed away immediately, so that usually but one or two layers are present. Commonly, however, the internal periderm layers extend for only a limited distance (Fig. 96). The central portion of such a sheet of periderm may be parallel to the outer surface of the stem, but its edges curve outward so as to

intersect or abut upon the older, outer cork layers; thus a lenticular scale of cortical or phloem tissue is cut off.

As the stem increases in diameter with the consequent deep splitting of the outer tissue, including the periderm bands, more and more periderm layers are formed, each more deeply in the stem. Thus the newer layers are formed successively in the inner cortex, the pericycle, and the phloem (Fig. 96). In old stems all layers, after the first few, are formed

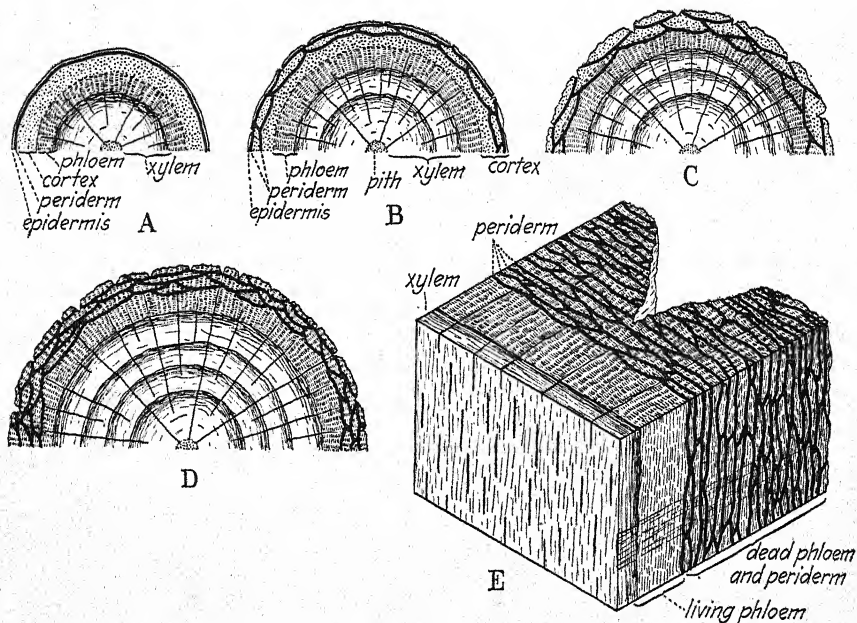


FIG. 96.—Diagrams, based on *Quercus rubra*, showing the position and extent of successively formed periderm layers in a typical woody stem. A, a one-year-old twig, the first periderm layer, a complete cylinder, formed beneath the epidermis. B, a two-year-old twig, the epidermis and first periderm ruptured; new, shell-shaped layers formed deeper in the cortex. C, a three-year-old stem, the outer tissues weathered away and more periderm layers formed still more deeply in the stem, invading the secondary phloem. D, a four-year-old stem, the cortex and outer secondary phloem with their periderm layers weathered away, the new cork layers invading the younger phloem. E, the outer tissues of an old tree-trunk, showing the narrow band of young, living secondary phloem, and the thick, deeply fissured layer of older, dead phloem with its many shell-shaped periderm layers; a considerable amount of similar tissue has weathered away.

in the newer secondary phloem; thus, in tree trunks the majority of periderm layers have formed in secondary phloem. The formation of each periderm layer shuts off all tissues to the outside from food and water supply; thus, soon after the initiation of a layer all outer tissues become dead. Possibly, the formation of a new periderm layer within is the factor controlling the length of activity of the previously formed phellogen. There is thus formed an outer crust of alternating cork and dead cortical or phloem tissue, these making up the so-called *rhytidome*, often

known as *shell bark* and *scale bark*. The German term *borke* is rarely used as synonymous with rhytidome.

The term *bark* has had many uses which have led to considerable confusion. Thus, in a non-technical sense, bark is applied to the tissues which are readily removed when logs or twigs are peeled, that is, to those outside the cambium. In a similar way both "bark" and "outer bark" have been used to designate the superficial layers of dead tissue made up of periderm and other tissues, and "inner bark" to designate the living phloem tissues next the cambium. The term "inner bark" has also been applied to the cambium zone itself. Periderm alone is sometimes called "outer bark," as in *Betula*, and sometimes "the bark." Some authors have used "bark" as synonymous with "cortex" in the technical sense, and still others use "outer bark" in this sense. The further use of the term "bark" in a technical sense is obviously inadvisable. The term may best be restricted to non-technical usage as designating all tissues outside the cambium, a usage already long-established. The more specific terms "cortex," "pericycle," "phloem," and "periderm" may well be employed in anatomical usage, and the term "rhytidome" may be used to indicate alternate layers of periderm and dead cortical or phloem tissues.

The age of the stem at which the formation of periderm starts is different in different species and under different environmental conditions. In woody twigs the first (outermost) periderm forms usually in the first season, the epidermis rupturing at that time. In some cases deeper periderm formation may also begin in the first year, but this is rare; the first layer often suffices for a few seasons, after which the deeper layers form. The apple tree and the pear tree begin to form internal periderm in the sixth to eighth year. Some species of *Populus* and *Prunus* retain their superficial smooth bark for twenty or thirty years or more, and, as before stated, *Fagus* and some other genera do not form internal periderm throughout the life of the plant.

All stages in the formation of periderm may therefore be observed in a tree of considerable age. In a pear tree, for example, early in the growing season the new shoots are covered with epidermis only. Extending down the stem from such shoots to a region six or eight years old is the zone covered by the first-formed superficial periderm, of epidermal origin, which gives a smooth, tan or gray-green surface. On the upper part of this zone the scaling remains of the epidermis may be seen. Below this is a comparatively narrow zone where the internal periderm has been formed in spots, but where the outer layers have not yet broken. A blotchy appearance is given to this region because of the discoloration of the dead tissue cut out locally by the internal periderm layers. The surface of these patches may be somewhat sunken because of the shrinkage of the dead tissue (Fig. 97, A). This zone shades gradually into a region of scaly bark where the outer scales have broken loose and are

dropping off (Fig. 97, *B*). Below this on large trunks the bark persists in ill-defined ridges, formed of periderm and dead phloem tissues.

The character of the older bark of different plants is dependent partly upon the extent and nature of the periderm layers, and partly upon the nature of the cortical and phloem tissues which are cut off by the successively formed phellogen layers. In many plants the outer phloem and the cortical tissues undergo extensive sclerification in which all parenchyma becomes converted into stone cells. This may take place in part before the tissues are cut off by the phellogen and in part after-

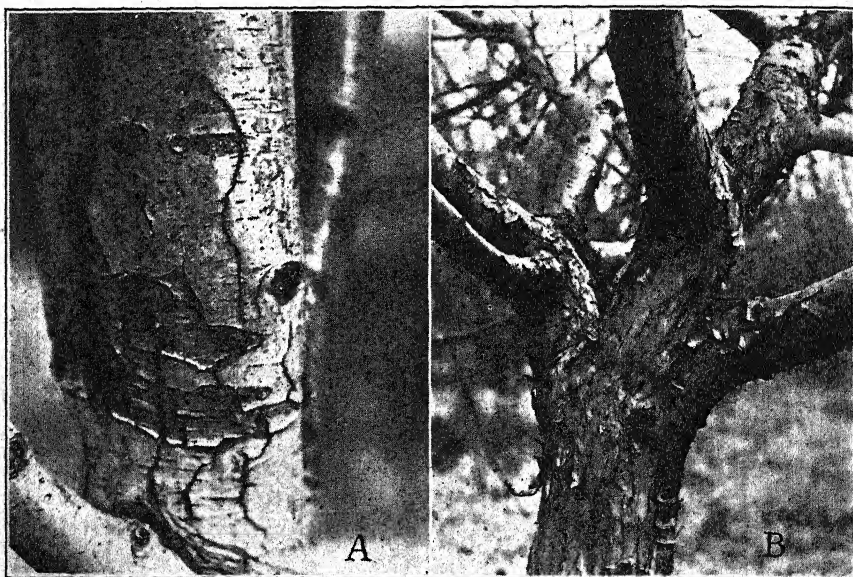


FIG. 97.—The trunk of young trees, *A*, *Pyrus communis*, *B*, *P. Malus*, showing the cracking and scaling of the outer tissues. In *A*, the smooth, continuous, outer periderm is cracking, and small, restricted, inner periderm layers are beginning to form, two of which, just below the center of the figure, have "cut out" and killed patches of outer tissue. *B* shows stages ranging from that seen in *A* to that where the trunk is freely scaling over its entire surface.

ward as the cells are dying. It is to these masses of sclerenchyma, together in some cases with firm or stony periderm cells, that different barks, such as those of species of *Quercus* and that of *Acer saccharum* owe their extreme hardness. Soft barks, such as that of *Magnolia acuminata* and *Ulmus americana*, result from the comparative scarcity of sclerenchyma masses and to the presence of soft cork layers.

Variations in the extent and firmness of the periderm layers account in large part for the different methods of bark exfoliation; thus the *scale bark* of the younger parts of the trunk of *Acer rubrum* and *Pyrus communis* is the result of the formation of small, isolated, periderm layers

which cut off scales of tissue. The breaking of the bark of the shagbark hickory, *Carya ovata*, into narrow, persistent strips attached by their upper ends is due to the method of splitting of long and narrow, vertical strips of periderm, and to the abundance of fibers in the phloem. In some of the red oaks the periderm layers are firm throughout and as a result the bark adheres tightly to the trunk without exfoliation, gradually disintegrating on the surface.

In some species the periderm forms definite abscission layers which cause the outer bark to be shed in sheets. Thus in *Platanus occidentalis* the outer bark over the trunk and larger limbs is cut off every spring. The "ring bark" of *Vitis* is shed in a somewhat similar manner, but in this case the outer tissues usually hang to the old vine in shreds for some time. These abscission layers of periderm have been described as belonging to two types, one in which a layer of thin-walled unsuberized cells is laid down by the phellogen between layers of firmer cork, and the other that in which thick-walled lignified cells are formed between layers of thin-walled cork tissue. Either type would cause the periderm layer to split under the action of moisture upon the unsuberized tissue and the strain set up by the increase in the diameter of the stem.

Periderm is frequently present in monocotyledons, and is often associated with more or less suberized primary cortical cells to form rhytidome. The periderm rarely, however, contains cells in long, continuous, radial rows, as in the gymnosperms and dicotyledons, but in most cases is made up of "storied cork," in which the cells are in short, somewhat irregularly placed, radial groups. Such cork occurs in *Iris*, *Acorus*, and *Monstera*. Rhytidome is present in such forms as *Cocos*, *Aloë*, and *Cordyline*. In monocotyledons the protective tissues which take the place of the epidermis when this layer is ruptured are in nearly all cases wholly or in part primary cortical cells, secondarily suberized. Such hypodermal layers may serve alone, as in the Gramineae, Cyperaceae, Orchidaceae, Juncaceae, Typhaceae; or may be combined with periderm (of the irregular, "storied" type) to form rhytidome, as in *Dracaena*, *Yucca*, *Zingiber*, *Asparagus*, etc.

✓ **The Function of Periderm.**—The principal function of the periderm is protection from drying out, this being accomplished through the constant renewal of the protecting tissues as the older layers are ruptured by secondary growth. Cork layers, when of considerable thickness, may also afford a certain amount of protection against mechanical injury to the tissues beneath. In addition to these functions, the periderm layers serve for the protection of various specialized structures or plant parts. Thus in fruits and tubers a periderm layer frequently takes the place of a heavily cutinized or cuticularized epidermis, as in the russet apple (Fig. 92, C) and the common potato (Fig. 95). In some tropical fruits—for example, the sapodilla (*Achras Sapota*) or the sapote

(*Calocarpum mammosum*)—cork layers are particularly well developed and give the fruit a gray-brown, somewhat rough appearance. Cork layers also occur in the bud scales of deciduous trees, and as wings and ridges on many dry fruits (Fig. 131). They also occur rarely on leaves, as on the petioles of some species of *Ficus*.

One of the special functions of the periderm is the protection of wounds through the production of *wound cork*. About wounds or dead tissue in practically any part of the plant (but rarely in leaves), a phellogen layer may be formed in the layers of uninjured living parenchymatous tissues adjacent to the wound. This layer forms phellem and phelloderm in the normal way, thus sealing the wound. Such a layer not only prevents water loss from the wound, but also protects the healthy tissues against infection by fungi and bacteria. Cork is particularly resistant to the action of microorganisms. Tissue dead from any cause is usually shut off from that which is healthy by a periderm layer, or by a suberized layer formed from preëxistent cells which become chemically changed.

Lenticels.—In periderm layers there are, in most cases, certain small, restricted areas in which the cells are loosely arranged, small intercellular spaces being abundant, and where the thickness of the layer is increased because of the loose arrangement of the cells, their larger size, and possibly greater number than in adjacent parts of the layer. These areas are known as *lenticels*. They are conspicuous on twigs, and on other smooth-surfaced organs, as more or less raised, often somewhat corky spots, where underlying tissues break through the epidermis. Lenticels are of almost universal occurrence on the stems of woody plants. Only a comparatively small number of plants have been reported to be without them; among these are *Philadelphus*, *Tecoma radicans*, *Vitis vinifera*, and some other plants, mostly vines, which shed the outer layers of bark annually, thus maintaining new tissues in close relation to the outer air. Lenticels are also found on many roots and frequently on fruits. The purple lenticels of *Morus alba* are conspicuous on the orange-colored roots. The so-called "dots" on apples and plums are familiar examples of lenticels upon fruit.

The lenticel, as a complete structure, is a lens-shaped mass of tissue bulging into the cortical parenchyma on one side and causing the surface of the organ to be raised on the other (Figs. 98, 99). In these areas the phellogen, instead of forming normal cork tissue, gives rise to large numbers of thin-walled, unsuberized, more or less rounded, air-filled cells known as *complementary tissue*. These cells are only loosely attached to each other, so that abundant radial air passages are present. Two types of complementary tissue are recognized, one in which the cells are more or less firmly united, forming a fairly compact tissue, as, for example, in *Salix* and *Ginkgo*; and one in which the complementary tissue is com-

posed of almost wholly unattached cells, which give the tissue a powdery consistency. Examples of this latter type are found in the stems of

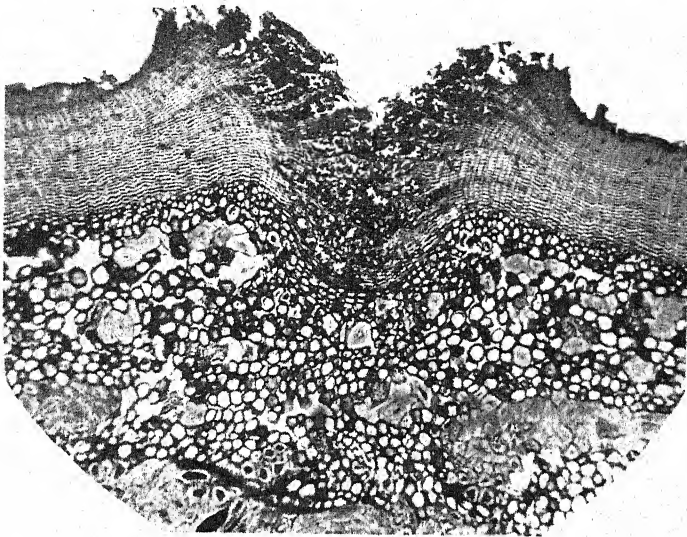


FIG. 98.—Lenticel of a young stem of *Prunus serotina* in transverse section of the stem, showing relation to periderm, alternate layers of closing and complementary cells, and the layering of the periderm.

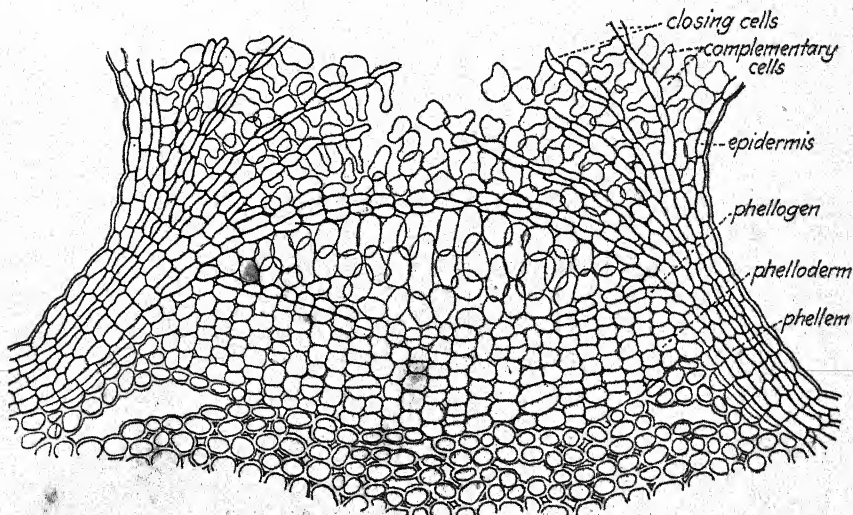


FIG. 99.—Lenticel of *Prunus avium* in transverse section of stem. A number of successive layers of complementary and closing tissue have been formed, and the large amount of phelloderm dips inward into the cortex. (After Deraux.)

Betula and *Prunus* (Figs. 98, 99), and in the roots of *Morus*. The masses of powdery complementary tissue are held in place by diaphragms of

denser tissue formed by the phellogen and known as *closing layers*. These layers, although sufficiently dense to hold the looser tissues together, are traversed by radial air passages, as is the phellogen layer itself. With the continued formation of new masses of complementary cells, the outer closing layers are broken through. This rupturing is in some plants most marked in the spring, when the projecting broken tissue is conspicuous.

The Origin of Lenticels.—Lenticels commonly originate beneath stomata (Fig. 100) on the young stems just previous to, or coincident with, the formation of the first periderm layer. In fact, inasmuch as the lenticel is itself a part of the periderm, the initiation of the periderm may be said to start with lenticel formation. In most cases the formation of the normal periderm spreads outward from the edges of the lenticel. The time of lenticel formation varies, of course, in different species according to the duration of the epidermis. In the majority of plants, however, lenticel formation occurs during the first season's growth and frequently even before growth in length has ceased. In the early stages of lenticel formation the cells immediately below the stoma, or group of stomata, divide in a number of different planes to form the first complementary tissue. (Such is not the case, of course, where the first periderm forms deep in the cortex.) These early divisions are followed sooner or later by the differentiation in the adjoining inner tissue of a normal phellogen layer which divides in the tangential plane only. The young complementary cells enlarge in size, lose their chlorophyll, and later their protoplasts, thus taking on the colorless appearance and light structure of mature complementary cells. With the formation of any considerable mass of such cells, the epidermis over the growing tissues is ruptured through the stoma (Fig. 100, A), exposing the masses of complementary tissue. With the continued growth of the phellogen, the epidermis around the opening of the lenticels becomes thrust back as flaps of tissue, and the pale masses of complementary cells protrude.

The Duration of Lenticels.—The duration of a given lenticel depends upon the formation of internal periderm. In those plants which form internal periderm early, the lenticel may be cut off and lost by the exfoliation of the outer tissues. On the other hand, in plants with persistent superficial periderm layers, such as *Betula* and *Prunus avium*, the lenticel may persist for a great many years. In such cases the lenticels become greatly elongated tangentially, due to the increase in circumference caused by secondary growth. This is also the case in some roots. The elongated lenticels of birch and cherry trees form conspicuous markings on the smooth bark. In such cases the phellogen layer of the lenticel is increased in extent by radial diversion of its cells at about the same rate as is that of the adjacent periderm.

With the formation of internal periderm new lenticels are formed by the specialized functioning of the phellogen, as is the case in the formation

of lenticels in the superficial periderm layers. Here the lenticels are so placed with reference to cracks in the outer bark tissues that gaseous

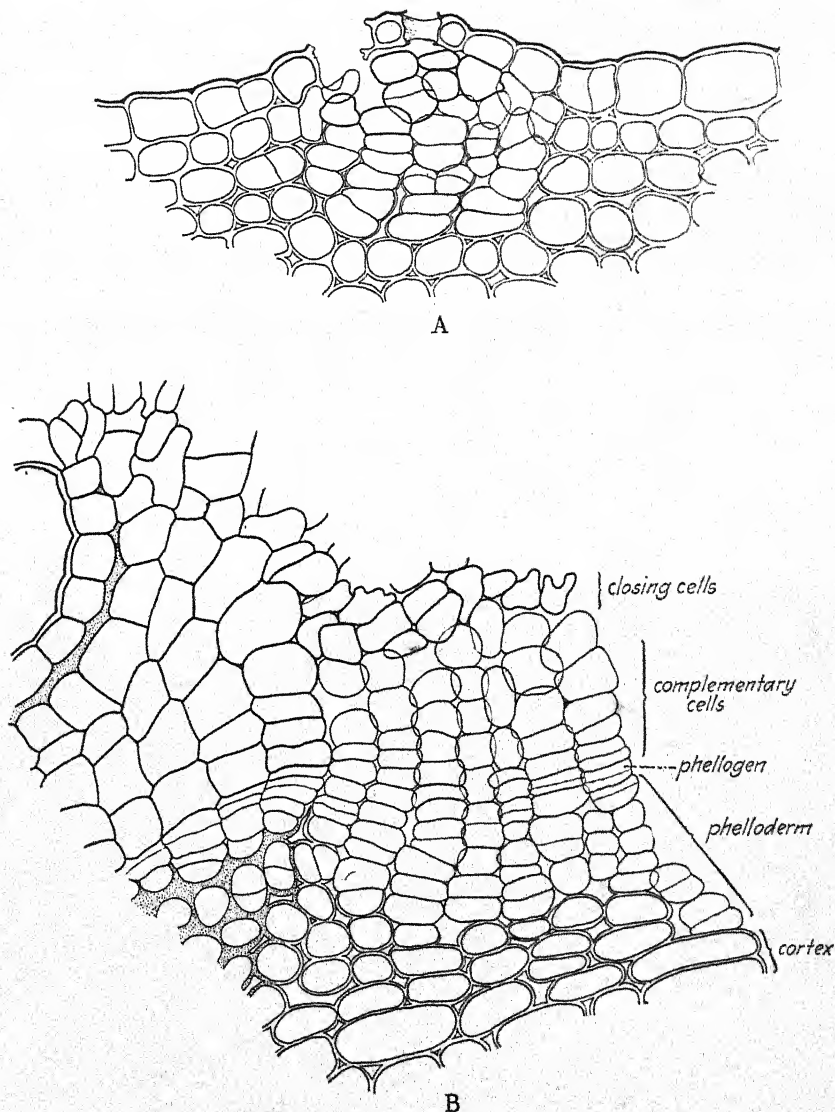


FIG. 100.—Early stages in lenticel formation. *A*, the lenticel phellogen has just arisen beneath a stoma, and the development of the first complementary cells has broken the epidermis. *B*, the enticel (only one-half shown) is well developed. (After Devaux.)

interchange is still possible through them. In *Quercus suber*, where the layer of phellem may be several centimeters thick, the lenticels persist, forming tubular masses of very loose complementary tissue reaching to

the surface (Fig. 94, B, C). It is this lenticel tissue which forms the spots of dark, porous, crumbling tissue in commercial cork. Because of the presence of these pervious radial cylinders of tissue, bottle corks are cut vertically from the cork sheet so that the lenticel tubes extend transversely through them. Very broad corks are cut radially, and are not "tight," because the lenticel tubes pass through them vertically.

The number of lenticels on any unit of surface area varies greatly with different species. In some it is dependent upon the number of stomata or groups of stomata; in others, however, lenticels may be formed in places between the stomata, if stomata are few; or if stomata are abundant, lenticels may form under only a small proportion of them.

Where the vascular tissue contains multiseriate rays, lenticels are found to be placed opposite these bands of tissue, suggesting that the ray and the lenticel together may form radial passages for gaseous interchange.

The commercial uses of cork are well known and are confined almost entirely to the cork of the cork oak, *Quercus suber*. The thin, tough sheets of cork from the canoe birch, *Betula alba*, and related species, have, of course, been important in the North American Indian civilization, but find little use today. The properties which make commercial cork valuable are the imperviousness of its cell walls to water, its lightness, toughness, and elasticity.

The Abscission of Leaves.—The pteridophytes and many herbaceous angiosperms, both monocotyledons and dicotyledons, retain their leaves after the death of these organs, and the leaves gradually decay or are torn away. But in the gymnosperms and the woody dicotyledons generally—less commonly in herbaceous dicotyledons and monocotyledons—the leaves are shed sooner or later by the formation of definite abscission layers. Though the details of abscission in these plants are unlike in different species, the fundamental structural modifications involved in leaf fall are the same in all cases. There is developed a well-defined *separation layer*, or *abscission layer*, which is the immediate structural cause of leaf fall, and also a *protective layer* which seals the underlying tissues against desiccation.

At the base of the petiole in the majority of species there is a short transitional region in which the sclerenchymatous tissues of the petiole and those accompanying the leaf traces are either reduced or wanting, and where the parenchyma cells have more dense cytoplasm. In this zone of tissue the *separation layer* is formed. This layer consists of the parenchyma cells of a narrow transverse band close to the base of the petiole (Fig. 101, A). This band is usually several cells wide, but varies somewhat in this respect in different plants. In this layer of parenchyma cells the *middle lamella* becomes chemically changed and breaks down or dissolves at the time of leaf fall. In some cases, and perhaps commonly,

the cellulose secondary wall also is affected; the outer layers of this wall dissolve, and only a thin, inner layer of cellulose remains about the protoplast. Chemically, the changes involved are apparently the conversion of cellulose into pectose, and of pectose into pectic acid and pectin. The pectic acid and pectin become gelatinous, and the calcium pectate of the middle lamella breaks down. The cells then become definitely separated from one another. All parenchyma cells of the region, including those of the vascular tissues, are involved in this change, so that the leaf is finally supported only by vascular elements. The abscission of the leaf

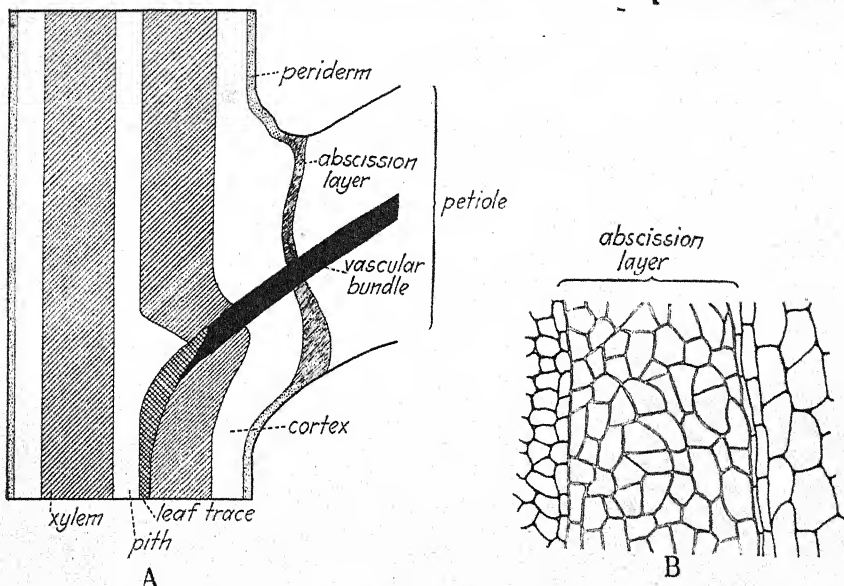


FIG. 101.—A, diagram to show leaf abscission layer; radial section through twig and leaf base in *Juglans cinerea*. The abscission layer extends through the vascular bundle only in parenchyma cells; all other cells are broken mechanically. B, detail of cellular structure of a small part of the layer three weeks before leaf fall; the cells of the region have divided a few times, the adjacent tissue being slightly compressed by growth of the new cells. No further changes occur until the cell walls begin to break down.

is then brought about by the mechanical rupture of the vessels, tracheids, and sieve tubes by the weight of the leaf and by wind and frost action. Minor variations from the above method of leaf abscission, which is that occurring in *Castanea*, are numerous. In some forms, such as *Juglans*, the cells of the separation layer divide a few times, without regularity of plane of division, before the cell-wall changes begin to occur.

The separation layer is often distinguishable days and even weeks before the leaf falls, as a layer of cells distinct from those above and below by different (usually smaller) size and shape, and by more dense cytoplasm. Further evidence of preparation for abscission is frequently to be found in the stoppage of the vascular tissues in and below this region by tyloses

and by gums of special types. In this manner protection is secured for the vascular strands.

Other tissues are protected by the formation of a layer of "ligno-suberized" cells just below the separation layer. In these cells the inner wall layer is suberized, the outer lignified. In the simpler cases, this layer is formed by the chemical transformation of the walls of the cells in the leaf base below the separation layer, without division among these cells, a condition found in *Acer* and *Pyrus*. In other forms, illustrated by *Prunus* and *Juglans*, the cells next the separation layer divide irregularly before the change occurs. In *Salix* and *Populus* a protective layer for the abscission wound is formed by the activity of a definite cork cambium; in these cases the cells of the protective layer are typically phellem. In the first two types also, periderm layers later arise deeper in the tissues of the leaf base to reinforce the protective layers. The next season these leaf scar periderms become joined with the stem periderm, completing the continuous corky covering of the stem.

The protective layer may be formed either before or after the fall of the leaf; periderm layers are formed after the protective layers develop, except in *Salix* and *Populus*, where the periderm layer constitutes the protective layer, and develops before the leaf is cut off. In some plants, as in *Tilia*, the old leaf scar itself is cast off the next season at the periderm layer, so that the periderm cylinder of the twig is smooth. These periderm layers over leaf scars form in the same way as does the normal stem periderm, the phellogen extending as a sheet of dividing cells through the living tissues of the old leaf base. In some cases phellogen cells develop even in the tyloses within the vessels, and thus the entire wound surface is effectively sealed with a layer of cork.

In those herbaceous plants in which abscission of leaves occurs, as, for example, *Coleus*, the method of separation of the leaf is essentially the same as in woody plants.

The Abscission of Branches.—Probably the most common example of branch abscission is the shedding of inflorescences and fruits, a phenomenon which occurs with nearly all plants. In some genera, to be sure—as, for example, *Rhus* and *Syringa*—the old flower and fruit clusters are not shed, but remain attached to the plant until they decay. In the majority of genera, however, these structures are cut off from the parent plant by definite abscission layers. Thus, in such plants as *Aesculus*, large flower and fruit stalks are shed by the formation of definite abscission layers which form in the living tissues at the point of attachment of the peduncle. This process is apparently closely comparable with that which occurs at leaf fall in the bases of leaves, since both leaf bases and peduncles have a considerable proportion of fleshy, living tissues. It is probable that in inflorescence abscission in general there is formed in the parenchyma an abscission layer the cells of which separate

readily, and the non-living vascular tissues are broken across mechanically. The surface of the wound is in most cases sooner or later protected by a periderm layer which forms a smooth scar except for the protruding, broken strands of xylem. The inflorescence scars of *Aesculus* are a familiar example. Similar abscission phenomena are found in the shedding of single fruits, such as apples and plums, and the cluster bases of pears. The cutting off of the tips of leafy shoots is characteristic of many genera which have indeterminate growth, such as *Ailanthus*, *Ulmus*, *Celtis*, and *Prunus* (plums). This abscission occurs chiefly while the twig is still green and succulent, but leaves a conspicuous scar. In some herbaceous plants, parts of the main axis as well as inflorescences and leaves may be cut off under special conditions. Thus the severed

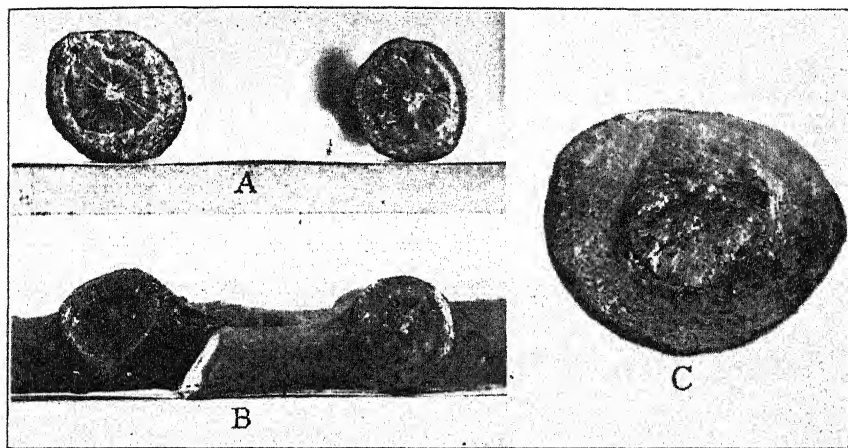


FIG. 102.—Branch abscission. A, B, *Populus grandidentata*; A, convex ends of recently shed branches; B, concave branch scars. C, end of large branch of *Agathis australis*. (A, B, natural size; C, $\times \frac{1}{2}$.)

stems of *Bryophyllum* when left to dry on a laboratory table have been observed to lose all appendages and the upper part of the main stem by abscission. In such abscission the cells of the separation layers probably undergo changes similar to those described for the separation layer of leaves, in which gelatinization of the middle lamella and of part of the secondary wall takes place.

In the above-described cases of branch abscission only those branches have been considered in which a relatively small proportion of hard vascular tissue is involved. In these plants the separation layers form in relatively fleshy living tissues and the xylem is ruptured mechanically. In some woody plants, however, strands or cylinders of vascular tissue of considerable size are cut off naturally by abscission layers which apparently extend through the xylem. Thus, in *Agathis* (Fig. 102, C),

branches even two inches or more in diameter are shed, leaving smooth scars on the tree trunk. Similar phenomena, involving branches of smaller size, are found in species of *Ulmus*, *Populus* (Fig. 102, A, B), *Quercus*, *Dirca*, and in other woody plants, both gymnosperms and angiosperms. The mechanism and the histological changes involved in such abscission have apparently not been extensively studied and in many cases are not well understood. In general, they are similar to those involved in leaf fall, in that there is usually the formation of a definite separation layer through which the rupture occurs, and the wound thus formed is later protected by the formation of a periderm layer.

In *Populus grandidentata* many of the smaller limbs are swollen at the base where they are attached to the trunk or main branches. This swelling consists largely of a thickened fleshy cortex in which stone cells, but no fibers, are present. The xylem cells in this region are conspicuously modified, as compared with those of the normal internode, in that the vessels are closely pitted in a scalariform or reticulate manner, whereas the normal vessels have crowded circular pits. Further, the vessels, fibers, and other cells are not lignified, their walls apparently consisting of cellulose. Parenchyma cells are also more abundant in this abscission zone of the xylem than elsewhere in this tissue. Through the living cells of this zone—both of the xylem and of all other parts—the abscission layer is formed, as in leaves at time of leaf fall. The parenchymatous tissues of the cortex and phloem separate easily, and the non-lignified vessels and fibers, already weak owing to their chemical nature, are readily ruptured because of the transverse, scalariform pitting. Following the fall of the branch, a periderm layer is formed within the living tissues of the branch base close to the main axis. Either by mechanical force or by dissolution, this layer cuts off the ends of the already broken scalariform vessels and extends as an unbroken sheet across the entire wound area, becoming continuous on all sides with the periderm layers which cover the main axis. Similar periderm layers form in *Dirca palustris*.

It is probable that abscission phenomena such as are described above occur in a considerable number of plants. There are, however, others, as, for example, those which occur in *Salix nigra*. Here no definite abscission layer exists, but just above the base in the smaller branches there is a weak zone through which rupture occurs very readily. Examination of this region reveals the fact that the cortex is considerably thicker here than in the normal internode, and the tissues outside the cambium are wholly lacking in fibrous sclerenchyma, whereas these strengthening cells are abundant in the cortex and phloem elsewhere in the twig. The xylem in this region is also modified, being less lignified than normally. Owing to this condition the fracture of the xylem occurs straight across the grain, and in this case the fall of the branch is not

followed by the formation of a smooth periderm layer. The dead stub usually persists until buried by the secondary growth of the axis. Other methods of branch abscission doubtless also occur.

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CHAPTER X

THE ROOT

That part of the plant axis which normally develops beneath the surface of the soil is commonly called the root as distinguished from the aërial portion of the axis, the stem. There are, of course, roots that are aërial and stems that develop underground, but in the main the distinction is valid. From the standpoint of anatomy, however, there are differences between root and stem which are fundamental in that they are concerned with the arrangement and method of development of the primary tissues. Thus the primary xylem in the root is exarch, as contrasted with the endarch condition in the stem (typical of gymnosperms and angiosperms), and the root has radial arrangement of vascular tissue, with alternating strands of xylem and phloem, whereas the bundles of stems are collateral, bicollateral, or concentric. Roots differ further from stems in that the former do not have appendages comparable with leaves, do not give rise directly to flowers, lack stomata, and form lateral branches from relatively permanent tissue in the pericycle, rather than from the promeristem at the growing point. Other differences are the presence of the root cap, a structure wholly lacking in stems; the almost universal occurrence of an endodermis, which is frequently lacking in stems; and the usual pericyclic origin of the initial periderm layer in roots, a condition found only rarely in the normal aërial axis.

Function of the Root.—The function of the root is twofold. Physiologically it is the absorbing organ of the plant, taking up water and mineral salts in solution and conducting them to the stem; mechanically, the root anchors the plant, and in most plants holds the stem erect in a way that makes possible the support of a large leaf surface. Absorption takes place for the most part by diffusion through the walls of the root hairs, although in some cases—for example, species of *Ranunculus*—root hairs are wanting, and water enters the root directly through the thin-walled epidermis. Water may be also absorbed through the epidermis of the root in the region distal to the zone of root hairs. Usually the older roots and those in which secondary thickening has taken place are incapable of absorption and serve only for conduction, support, and storage. Roots are adapted to their rôle as supporting organs by their tensile strength, their flexibility, and their extensive ramification through the soil.

Origin of the Primary Root.—The continuation of the axis, as the main root, is often called the *primary root*, all branches of this being

secondary roots. Primary and secondary roots differ in their mode of origin. The primary root is present in early stages of the seedling, in some cases in the embryo within the seed. The apical growing region of the primary root is developed as a part of the differentiation of the embryo, one end of the axis possessing root structure, or at least root-tip meristem. The origin of secondary roots as lateral structures is discussed later in the chapter. Between the root and the stem, a transitional region is formed in which the exarch xylem and the radial structure of the root pass over into the normal stem structure. The anatomy of this region is discussed in Chap. XI.

The Root Cap.—The promeristem, or growing region, of the root is near its apex. Here rapid cell division takes place and the general axis structure is laid down (Chap. III). In the pteridophytes there is usually a single apical initial which cuts off cells in a number of planes. In the seed plants generally, there is a group of initials taking part in the formation of the axis proper. (In either case cells are cut off by the apical cells not only away from the direction of growth, but also ahead of the meristem. These latter cells are relatively few in number and form a cap-like structure over the tip of the growing region, which is known as the *root cap* (Figs. 25, 28). The root cap is characteristic of roots. In origin it shows considerable variation: in some cases there is a definite initial layer, or *calyptrogen*, formed early in the ontogeny of the root, which constantly renews the root cap from within as its outer parts are lost; in others the cap is renewed by the division of cells in the dermatogen or in the outer layers of the periblem; in still others it is formed directly by the principal initial cell or initial cells which cut off root-cap cells toward the apex. The root cap persists throughout the growing life of the root and serves to protect the apical meristem as it is forced through the soil. The cells at the very apex of the root cap are usually only loosely united and are sloughed off continually. Root caps are lacking in most aquatic plants, in parasites, and some other specialized types of plants.

Ontogeny of the Root.—Behind the apical cells there is a region of rapid cell division and elongation (Fig. 25). In this region, as in the corresponding region in stems, the foundations of the primary structure are laid down and first become evident in the three general regions known as the dermatogen, periblem, and plerome. The fact that these regions are without constant morphological significance has been brought out in Chapter III. The terms may, however, be usefully applied as distinguishing certain regions in the ontogeny of the axis, particularly of the root, where these regions are generally more or less definitely set off and are not confused, as in the stem, by the formation of branches and appendages.

The region of elongation in roots is not of such great extent as that in stems, a condition which is probably an adaptation to the difficulty of growth through the soil. By the increase in the size of the cells in this

region the root tip is forced through the soil, the direction of growth being determined locally by obstructions, and in general by the geotropic and chemotactic responses of the root tip. As soon as elongation ceases, the tissues become permanent and no further longitudinal increase is possible.

The mature primary tissues differentiated in roots are essentially similar to those found in stems. Thus the outer layer is the epidermis, and beneath this, in some cases, is a more or less well-developed hypodermis (Fig. 103, A), or subepidermal layer, of cortical origin. Beneath this, in order, are the normal cortex, endodermis, and pericycle, which are cylin-

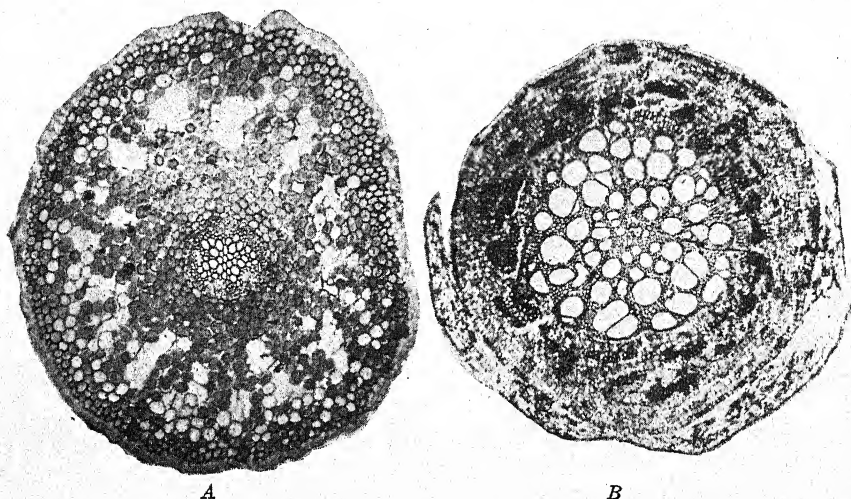


FIG. 103.—Root structure, as seen in cross section. A, a root without secondary tissues, *Ranunculus acris*; the protostelic central cylinder is pentarch; the parenchymatous cortex is fleshy, with large intercellular spaces, its outer layers have become suberized and form a hypodermis; the epidermis and subepidermal cortical cells are decaying. B, a woody root, with large amount of secondary tissues, *Populus deltoides*; a periderm has formed in the 'pericycle,' and the cortex is sloughing off. (The central parts of similar roots are shown enlarged in Figs. 104, D and 105, A, respectively.)

drical layers of tissue enclosing the strands of xylem and phloem. Pith is typically absent in roots.

Root Hairs.—The most characteristic features of the epidermis of roots are the uncutinized cell walls, the lack of a cuticle, and the root hairs (Fig. 53), which are the specialized absorbing organs. In the great majority of plants, root hairs are confined to a part of the root just behind the region of elongation. Generally, they persist for a short time only, the older root hairs withering away and new ones being formed farther along the root as the root tip increases in length. Thus the root hairs mature progressively farther and farther away from the base of the root, and in this way are constantly coming into contact with new soil. In

certain plants, particularly some specialized herbs and plants of aquatic habitat, root hairs are wanting.) Even roots on which root hairs would normally be present in soil may lack them when grown in water. On the other hand, a considerable number of plants—as, for example, *Gleditsia triacanthos* and *Eupatorium purpureum*—have persistent root hairs, which may be generally distributed or may be confined largely to the proximal parts of the roots. The presence of persistent root hairs is correlated with the comparative absence of secondary growth and the lack of periderm formation. Soon after the root hairs cease to function and wither away, the epidermis, or often the hypodermis, becomes suberized and forms a protective layer for the older root.

In the formation of a root hair the outside wall of the epidermal cell grows out to form a slender tubular structure somewhat resembling a pollen tube. The cell wall is very delicate and translucent, giving the root hair a white appearance. The protoplast of the epidermal cell extends into the tubular expansion as a lining of cytoplasm over the entire wall, which surrounds large interior vacuoles. The nucleus is usually present near the middle or the distal end of the tube. In water or moist air, where no firm obstacles are encountered, root hairs are straight and assume a position at right angles to the root axis. In the soil, however, they may take on any shape, their form being dependent upon the contacts with the soil particles (Fig. 53). Frequently, the root hairs become more or less firmly attached to the soil particles, so that the particles cannot easily be removed, even by washing.

The Cortex of the Root.—The cortex of most roots consists wholly or largely of relatively unspecialized parenchyma (Figs. 103, 104). As compared with the cortex of the stem, the root cortex is usually thicker in proportion to the size of the axis, a condition perhaps brought about as an adaptation to the function of storage. In some fleshy roots the thickness of the cortex is many times that of the stele, which appears as a slender thread or core extending through the spongy cortical tissue. Generally, the cortex of the root is not so firm as that of the stem of the same species, in that sclerenchyma is relatively small in amount or wanting in the root. Also the cortical tissue of roots is not so dense, having more intercellular spaces than that of stems. Secretory cells, resin ducts, and similar structures are normally present in the root cortex of many species. Special structures adapting the cortex to particular function or environment often occur. In roots which have no secondary thickening the cortex may persist for a number of years or throughout the life of the root. Such is the condition in the roots of monocotyledons, pteridophytes, and many of the herbaceous dicotyledons. Naturally, when secondary thickening takes place to any extent, as is the case in woody dicotyledons and gymnosperms, and in many herbs, or when an internal periderm layer is formed, the cortex is soon destroyed.

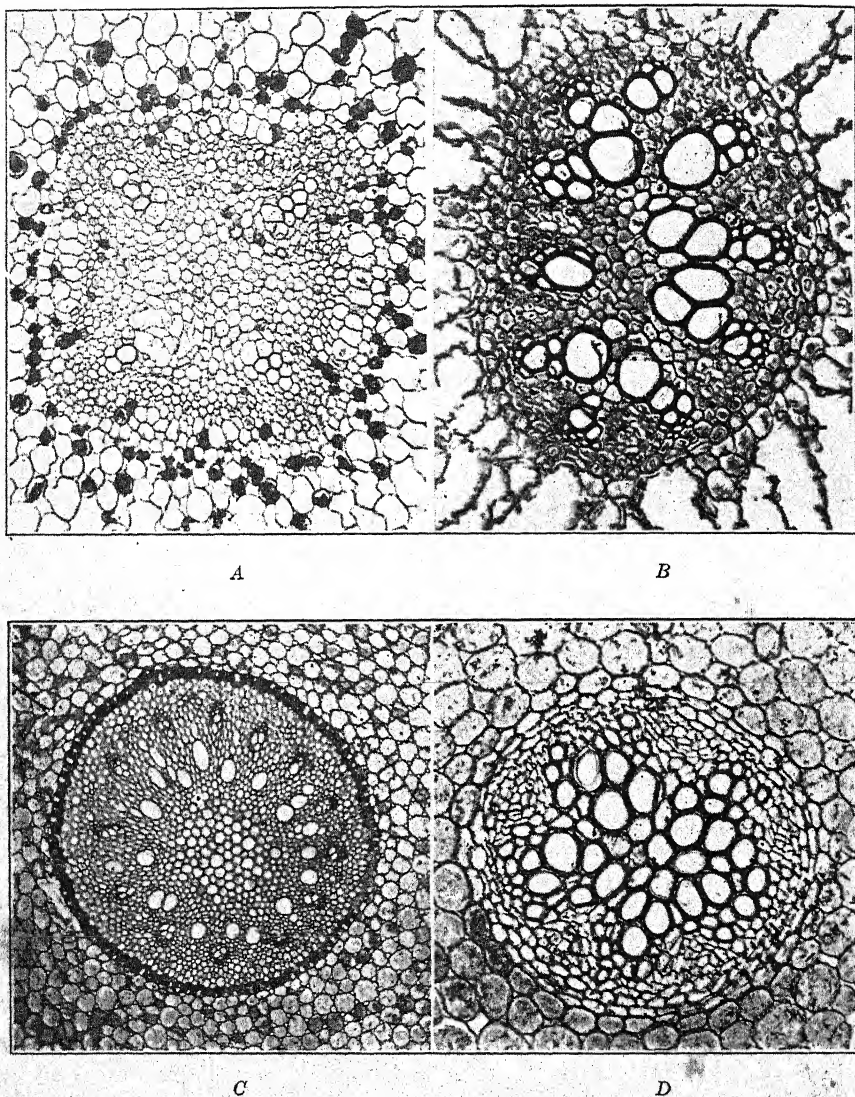


FIG. 104.—The primary structure of the stele of roots. A, young root of *Salix nigra*, tetraarch; only the outer parts of the xylem strands are mature; the phloem is hardly separable from the parenchyma and the procambium; the thin-walled endodermis is evident. B, polyarch root of *Polygonatum biflorum*; a small, irregular pith is present; the phloem and the endodermis are seen indistinctly set off from surrounding cells. C, polyarch root of *Smilax herbacea*; the phloem strands are dark-stained; the xylem strands are distinguishable with difficulty from the sclerenchyma in which they are embedded, but the darker-stained protoxylem region and the large innermost vessels limit the strands; a large pith is present; the thick-walled endodermis is prominent. D, pentarch root of *Ranunculus acris*; no pith is present.

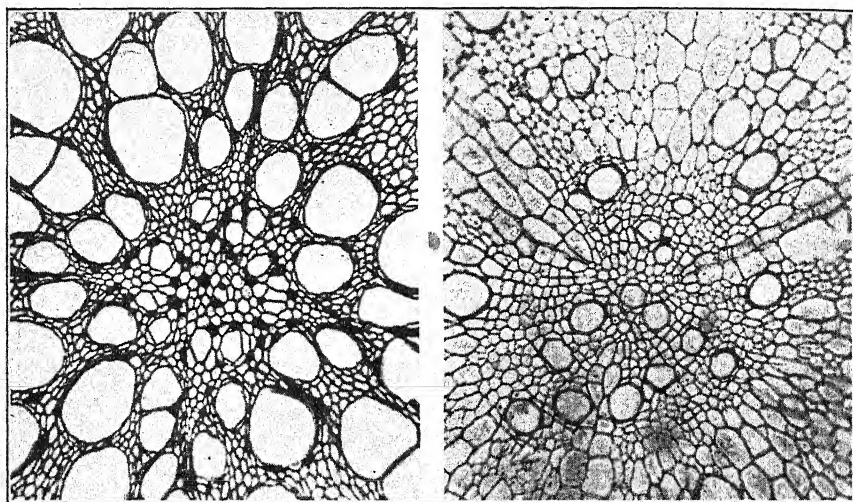
Limiting the cortex on the inside, and frequently considered to be a part of it, is the endodermis (Fig. 104). This layer is present almost without exception in the primary body of roots. Its structure and its function have been described in Chapter V. The endodermis is, of course, destroyed soon after the incidence of secondary growth. In the majority of species, therefore, its functioning life is short.

The Pericycle of the Root.—The pericycle of roots, as compared with the cortex, is a relatively narrow zone of tissue. Its component cells are largely parenchymatous in nature, and, although they become permanent tissue early in the development of the root, they retain their ability to initiate new structures by the formation of secondary meristems. It is in the pericycle that lateral roots are initiated, and, in the majority of cases, the first periderm layer is formed. In many roots the pericycle as seen in transverse section, is an unbroken ring of tissue. In a few plants, however, the bands of primary xylem abut upon the endodermis, in which case the pericycle is divided into as many segments as there are arcs of xylem. The pericycle is commonly a persistent structure in roots even where secondary thickening is fairly well developed. In such cases new cells are added by the division of the existing parenchyma so that the layer is not ruptured by the growth beneath it, and appears much as does the cortex of stems after growth under similar conditions. With continued secondary growth in the older roots of woody plants, periderm layers are formed in the phloem, and the pericycle is thus lost.

The Primary Vascular Tissues of the Root.—Because of the radial arrangement of the strands of primary xylem and phloem which is characteristic of roots (Fig. 104), there are no concentric zones or rings of these primary tissues in roots similar to those found in stems. The xylem, as seen in transverse section, occurs as radially extending groups of cells with the first-formed protoxylem situated at the outer ends of the rows of cells (Fig. 104). Thus in the development of the strands of primary xylem the first cells of the procambium strand to mature into xylem are those situated in the pericyclic region next the endodermis. From this point xylem cells are matured progressively towards the center of the stele (Fig. 104, A), until in the majority of cases they abut against those of the other xylem groups (Figs. 103; 104, D; 105). In this way the meristematic cells in the center of the stele commonly develop somewhat late into xylem cells, and a pith is absent. The roots of the monocotyledons frequently possess pith (Fig. 104, B, C), as do those of numerous other plants, especially herbs. Tap roots and other large main roots may possess pith even when other roots of the same plant are pithless. Where a pith is present, the central meristematic tissue has developed into parenchymatous tissue instead of xylem.

The number of arcs of xylem varies through rather wide limits in different groups of plants (Figs. 104, 105). Thus in the roots of mono-

cotyledons a large number of radial plates of primary xylem, for example, fifteen or twenty, is often found. In most dicotyledons, both woody and herbaceous, and in the gymnosperms, relatively few primary xylem strands are present. Pteridophytes also have few strands. Roots are known as *monarch*, *diarch*, *triarch*, *tetrarch*, *pentarch*, etc., and *polyarch*, when the number of xylem groups is one, two, three, four, five, and many, respectively (Figs. 104, 105). The number of xylem and phloem strands is to some extent constant for a species. However, most species show considerable variation, being either diarch or tetrarch, or triarch or



A

B

FIG. 105.—Central portions of protostelic roots with secondary thickening. A, a woody root, *Populus deltoides*, tetrarch; the small-celled, tapering protoxylem tips of the primary xylem ridges project far into the secondary xylem, which closely surrounds the primary xylem, no definite line of demarcation being visible except about the ridges. B, a storage root, *Tephrosia virginica*, triarch; the primary xylem is small in amount, with a median vessel; the protoxylem points lie at the ends of the wide parenchymatous wood rays; the secondary xylem consists largely of parenchyma.

hexarch, for example; less commonly triarch or tetrarch, pentarch or hexarch. Often the different roots of an individual vary in structure—in some pines, for instance, the vigorous and main roots are tetrarch, the others diarch; in individuals of other species of pine, hexarch and tetrarch roots occur.

Spiral and annular elements are not found so frequently in the protoxylem of roots as in that of stems, and when present are fewer in number, probably because of the fact that the region of elongation in roots is relatively short, and because in roots very few xylem elements mature during the elongation stage, developing rather in the zone of growth just behind this, where there is no elongation. The region of elongation of

rapidly growing stems may be 8 or 10 cm. or more in length, whereas that in roots may be only a single centimeter, more or less. The region where greatest absorption takes place, namely, that normally covered with root hairs, is behind the zone where growth in length takes place. Water-conducting elements capable of elongation would, therefore, be of no particular value there, as the conditions to which they are an adaptation do not exist. It is evident that in the stem the function of ringed and spiral elements is to conduct water and nutrients to the growing tip. The root tip, on the other hand, is surrounded by moist soil and absorbs water and nutrients directly. Food materials must, of course, be conducted from stem to root tip through the phloem and parenchymatous tissues.

The primary phloem of roots occurs as strands of tissue lying between or alternate with the radially extending plates of xylem (Figs. 104, 106). As a rule, the groups of primary phloem cells as seen in transverse section are more or less rounded or somewhat triangular in shape and are separated from the xylem groups by parenchymatous tissue. Frequently, the phloem groups are not well defined but merge into the surrounding parenchyma which they resemble in cell types. The direction in which the protophloem cells mature is in most, perhaps all, cases centripetal. The order of development apparently has no morphological significance and no types are recognized as in the xylem.

The primary phloem of roots consists of sieve tubes, companion cells, and parenchyma, and differs in no fundamental way from that of stems. As with all primary phloem in plants where secondary tissues are formed, the size of the elements is small compared with that of normal secondary phloem cells. The phloem of monocotyledonous roots is ordinarily more distinctly set off from the surrounding parenchyma or sclerenchyma than is that of other groups.

Secondary Growth in Roots.—In roots which have secondary thickening the cambium originates as bands or strips of meristem in the procambial or parenchymatous tissues between the groups of primary phloem and the center of the stele (Fig. 106, A). Here short tangential rows of initials are formed which cut off secondary xylem cells toward the inside and phloem cells toward the outside according to the normal method of cambium activity (Chap. VI). From the ends of these first-formed cambium segments the layer of initials is extended laterally by the differentiation of the parenchyma between the primary phloem and xylem strands until the segments of cambium meet in the pericycle between the xylem and the endodermis (Fig. 106, B). Thus a continuous cambium sheet or cylinder is formed, which is not circular in cross-sectional shape because it bends out around the primary xylem groups and dips inward beneath the primary phloem. Secondary tissues are formed earlier by the segments of cambium inside the primary phloem,

and usually more rapidly in those regions, so that the cambium soon becomes cylindrical (Fig. 106, *D*). With the formation of the secondary tissues the primary phloem is crushed (Fig. 106, *B*, *C*) and the endodermis

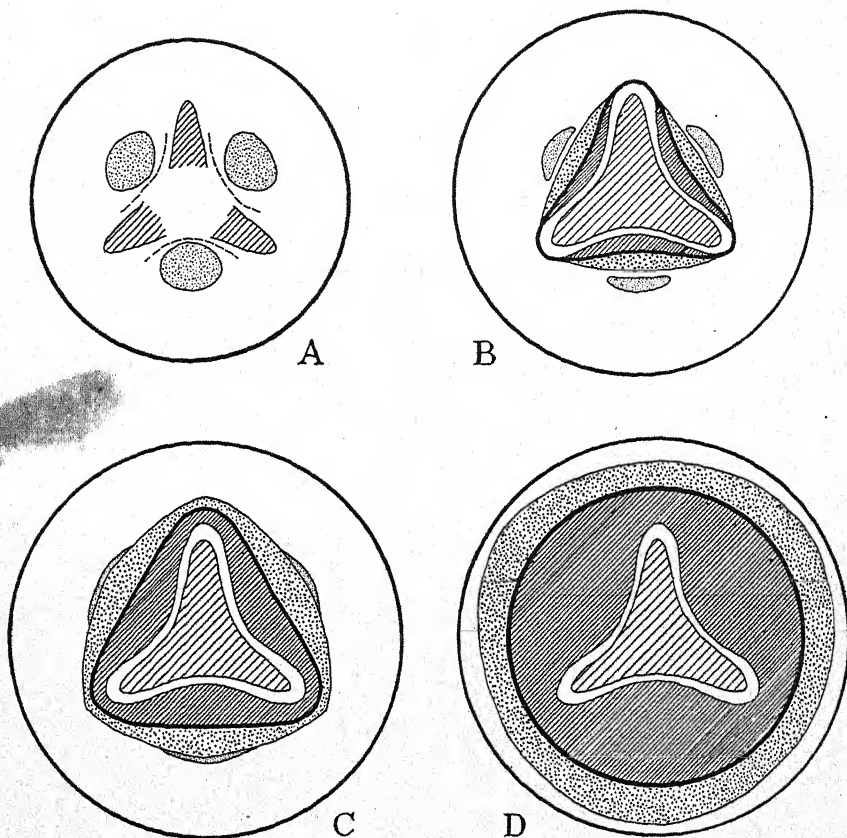


FIG. 106.—Diagrams to show origin of secondary growth in roots, the primary xylem lightly cross-hatched, the secondary closely; the primary phloem finely stippled, the secondary coarsely; the cambium represented by a heavy line; the endodermis and other layers not differentiated. *A*, young root; the inner xylem not mature; the cambium arising in the positions shown by the dotted lines. *B*, the cambium has formed secondary xylem and phloem beneath the primary phloem, the regions where it first appeared, and has developed laterally, surrounding the tips of the xylem ridges, where no tissues have yet been formed; the primary phloem is crushed. *C*, secondary growth has continued, tissues forming about the ridges completing the three-angled cylinder of secondary xylem and phloem; the primary phloem is still further crushed. *D*, with continued secondary growth the cambium cylinder has become round in cross section; the primary phloem has disappeared. (A band of parenchyma is shown between primary and secondary xylem; this is often lacking.)

ruptured. The crushed cells are usually soon absorbed. The primary xylem, however, remains intact, being readily visible in older roots, surrounded by secondary xylem (Fig. 105).

The secondary vascular tissues of the root do not differ fundamentally from those in the stem. Such differences as do occur are apparently the result of adaptations to differences in function, the stem being adapted to the support of a large leaf surface in dry air and the root to anchorage in moist earth and to storage. The xylem of roots, as compared with that of stems, has larger and more numerous vessels with thinner walls, fewer fibers, more parenchyma, and larger or more abundant rays (Fig. 107); the phloem, less sclerenchyma and more storage parenchyma. The arrangement of xylem and phloem elements in the secondary tissues of roots is fundamentally the same as that found in the stems of the same species.

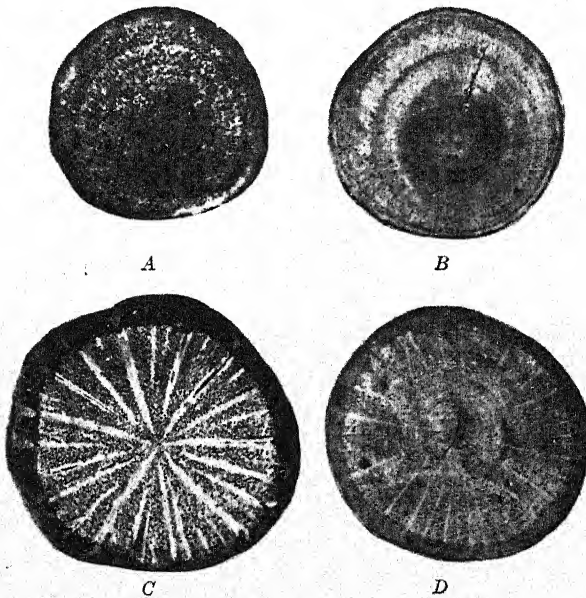


FIG. 107.—Root and stem wood. A, B, of *Morus alba*. C, D, of *Quercus velutina*. Showing larger and more abundant vessels and rays in the root. ($\times 2$.)

The Formation of Lateral Roots.—As previously stated, one of the characteristic features of roots as distinguished from stems is the method of formation of lateral appendages of the axis. In stems, the primordia of the branches and leaves are laid down in the primordial meristem at the growing point, according to a definite plan. In roots, on the other hand, no branches or appendages of any kind are laid down in the meristem at the root tip, and when lateral roots are developed they are initiated in relatively permanent tissues and without regular order with reference to each other, except that of general acropetal succession. Lateral roots are commonly formed most abundantly in the region just behind the zone of root-hair growth. As they extend at right angles to

the axis of the root from which they are derived, and in turn produce root hairs, and later, lateral roots, it is apparent that the branching system thus formed is very effective in reaching all parts of the soil.

The origin of lateral roots is endogenous, that is, the root meristem is formed in the inner tissues of the mother axis, and appears externally

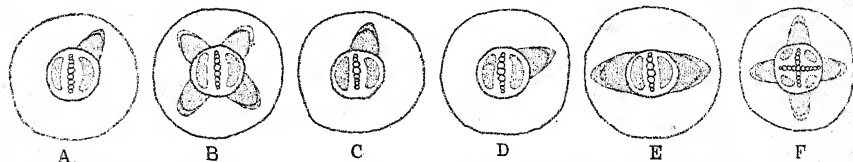


FIG. 108.—Diagrams to show position of origin of lateral roots. A-E, various positions found in gymnosperms and angiosperms whenever root has less than three xylem "rays." F, position (opposite xylem "rays") found in all pteridophyte roots and in roots of other vascular plants whenever there are three or more xylem "rays." (After Van Tieghem and Douliot.)

only after growth of the organ is well begun. In angiosperms and gymnosperms the meristems arise in the pericycle just beneath the endodermis; in pteridophytes growth begins in the cells of the endodermis. In both cases the originating cells may have attained the permanent stage, or may be in the later stages of development. In gymnosperms

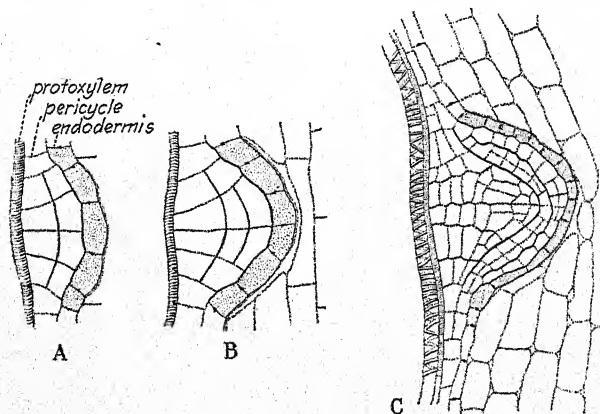


FIG. 109.—Early stages of lateral root development, radial section; *Hypericum*. A, a group of cells of the uniseriate pericycle have enlarged radially and divided tangentially. B, further enlargement and division have occurred; the endodermis and inner cortex are stretched. C, the root-tip meristem is well established; the endodermis will soon be ruptured. (After Van Tieghem and Douliot.)

and angiosperms the points of origin of lateral roots are opposite the xylem "rays" whenever there are more than two of these strands (Figs. 108, F; 110, A, B); in the pteridophytes they are in all cases opposite the xylem strands. Where in the first groups the root is diarch, there are usually four positions of possible lateral-root origin, each so placed that the rootlets depart at an angle with the xylem "rays" (Fig. 108, A-E).

The location of these points varies, but is usually between the xylem and the phloem strands. The restriction of lateral-root formation to the regions opposite the xylem causes these roots to appear in vertical rows, as many rows of laterals being formed as there are rays of xylem. Thus a

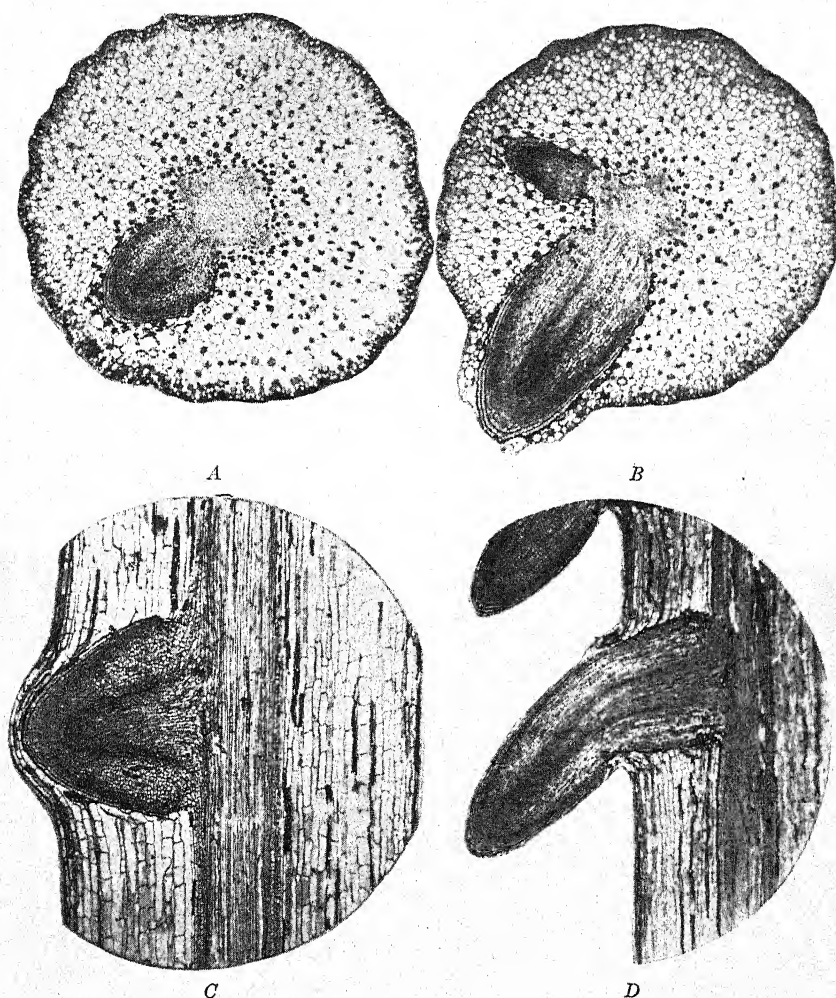


FIG. 110.—Late stages of lateral-root development, *Salix nigra*. A, B, transverse sections; C, D, radial sections. A, the tip of the young lateral root is passing through the cortex; in B, it has forced outward the outer cortical layers and the epidermis, and broken through. C, the lateral root tip is about to break through the outer cortex. D, the lateral root is free from the mother root; its attachment to the central cylinder is obvious.

tetrarch root has four rows of laterals. In the case of roots not located opposite rays of xylem, definite rows are likewise formed. This longitudinal-row condition is often readily visible in such storage roots as those of the radish, parsnip, and turnip; it may also be seen in the roots of willow

and other plants which grow in water. The regularity of arrangement is distorted in soil, unless the diameter of the main root be large.

Where a lateral root is to be formed, the cells of the pericycle of an area (circular as seen in tangential view) at least two cells in diameter become meristematic. These cells at first increase in radial diameter, then all divide tangentially (Fig. 109, A). Succeeding divisions may be in any plane. A definite growing point with its initial cells, root cap, and other characteristic structures is quickly formed. As this meristem develops, the outer tissues are stretched (Figs. 109, B, C; 110, C) and then soon ruptured (Fig. 110, B). The root forces its way, apparently partly by absorption of the surrounding tissue, but in large part by mechanical pressure, through the endodermis, cortex, and epidermis, and continues growth in the normal way. In many cases there is said to be a partial chemical dissolution of the cortical tissues by the root cap as it forces its way out. There is no connection between the epidermal cells of the root and the disrupted tissue of the cortex through which it passes. At the proximal end of the lateral root, however, where the meristem was initiated, there are adjustments which provide for the conduction from the lateral into the main root, although no actual union of the primary xylem tissues takes place. With the formation of secondary growth a cambial connection is made with the main root, and annual rings of tissue are laid down which are continuous over the point of insertion of the lateral. Not all laterals grow with the same rapidity; some persist and grow rapidly, forming part of the main root system of the plant, whereas others remain small or are lost altogether. In some plants, and especially in storage roots, there is a seasonal renewal of secondary rootlets.

Adventitious roots develop by the formation of apical root meristems in the pericycle of stems and roots, or, in older axes, where the pericycle is no longer active, in the secondary phloem. The growing root then forces its way through the outer tissues. In some of the pteridophytes, and rarely in the angiosperms, adventitious roots are said to arise from the cells of the outer cortex. It is possible that such "roots" are, however, haustoria, or other emergences.

The Periderm of Roots.—Sooner or later in the development of the majority of perennial roots a periderm layer is formed. This is especially true in the dicotyledons and gymnosperms where secondary thickening takes place. It will be recalled that in stems the first-formed periderm usually arises in the epidermis or in the cortical layers immediately beneath. (In roots, on the other hand, though suberization of the outer layers may take place, the first true periderm commonly arises in the outer layers of the pericycle, and in woody plants persists as a continually expanding layer for a considerable number of years. In such cases the endodermis and cortex are ruptured and soon decay, so that the root has a

smooth, brownish covering of cork cells broken only by the lenticels.) These structures do not occur conspicuously in all species, but in some—as, for example, *Morus* and *Gleditsia*—appear as tangentially elongated roughenings of the root surface. The structure of root lenticels is not fundamentally different from that of the lenticels of stems. As a rule, however, such lenticels are of greater tangential extent, owing to the increase in the circumference of the persistent periderm layer. A comparable condition is found in the superficial periderm layers of the trunks of species of *Betula* and *Prunus* in which tangential elongation of the lenticels takes place. In some species the accumulation of complementary cells is very apparent as a powdery mass in the lenticular cavity.

(In very large roots and in smaller roots of some species secondary periderm layers arise in the phloem tissues, and the pericyclic region is lost. New periderm layers may then arise progressively more and more deeply in the phloem tissues, as is normally the case in stems. There is, however, no extensive accumulation of bark on roots because of the rapid decay of all dead tissues beneath the surface of the soil. When roots are exposed, as is frequently the case with the upper side of roots at the base of a large tree, there is formed apparently normal bark, resembling that of the trunk proper.)

(Although the above situation with regard to periderm is the one most commonly found in roots, many exceptions occur. In those roots which have no secondary thickening, the epidermis may persist intact, often becoming cutinized; or the epidermis may be lost by decay and be replaced as the limiting layer by an outer primary cortical layer which becomes cutinized, as in many monocotyledons. In such cases the true epidermis may shrivel and disappear as soon as the root hairs cease to function. Such an accessory protective layer, serving as an epidermis, is sometimes called an *exodermis*. This is, however, merely a type of hypodermis, and the term “exodermis” is also applied to a uniseriate layer in certain specialized roots, for example, the innermost layer of the velamen of orchid roots. A persistent epidermis is especially common among the roots of the monocotyledons. In this group periderm forms the protective layer only in the larger, older roots, as in the Araceae and Liliaceae. In herbaceous dicotyledons a hypodermis is often the protective layer (Fig. 103, A). Periderm layers also frequently occur in the roots of such plants as in the Primulaceae and Gentianaceae; these layers occur in the outer cortex, but not superficially, as in the monocotyledons. In the pteridophytes, periderm does not form in the roots, but the epidermis and the outer cortical layers become cutinized or lignified without change in size or shape of the cells. The chemical nature of these lignified or cutinized walls is apparently unlike that in similar cells in most of the seed plants, since the staining reactions are different.

Unusual types of structure are found in roots as in stems, but in roots these are associated chiefly with secondary tissues. Very few unusual forms of primary structure occur in roots. Anomalous structure in roots is similar to that in stems and the description of anomalous stem structure in Chapter XI will serve for roots also.

Roots show great specialization as the result of adaptations to environmental conditions and to particular functions. Among the most striking variations are aërial roots, storage roots, holdfasts, and aquatic roots. A discussion of the modifications found in some of these will be found in Chapter XIV.

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CHAPTER XI

THE STEM

That part of the axis of a plant which bears the leaves and reproductive structures and is commonly aërial and ascending is called the stem. Stems and roots are alike in general structure, each possessing a stele with xylem and phloem, pericycle and endodermis, and a cortex with an epidermis. Stems differ from roots in fundamental vascular structure and in the possession of appendages borne at definitely fixed positions known as nodes. The difference in vascular structure lies chiefly in the arrangement of the xylem and phloem: in the root the strands of primary xylem and phloem lie in different radii, separated from one another; in the stem the strands lie side by side in the same radius. Further, the xylem of the root is always exarch, whereas that of the stem is exarch, endarch, or mesarch, being endarch most commonly in present-day plants. In the development and structure of secondary vascular tissues roots and stems are very much alike.

Origin of the Stem.—The first stem meristem develops during the specialization of the embryo. Lateral stems normally arise by the development of new apical meristems laterally in the terminal meristem of the mother stem. Adventitious branches develop, on both stems and roots, by the formation of similar meristems secondarily in the pericycle, phloem, or perhaps even in the cambium. In a few plants they are said to arise in epidermal or subepidermal cells. Branch meristems also develop freely in wound tissue of some species. Such meristems arise by the division of meristematic cells, or of more or less permanent parenchyma, in several planes, an apical growing point like that of the normal stem tip being formed. If this meristem is deeply buried in the stem tissues, it breaks its way through to the surface much as the lateral root meristem breaks through the root cortex. The course of development of the mature stem from meristem is discussed in Chapter III.

Root-stem Transition.—Root and stem form a continuous structure, the axis. There is, therefore, a transition region where root and stem meet, and where the various parts of each organ merge into those of the other. The cortex, endodermis, pericycle, and secondary vascular tissues are directly continuous from the root into the stem. The primary vascular tissues are also continuous, but not directly so, since the types of bundles and of arrangement are markedly different in the two organs—the radially arranged, independent strands of xylem and phloem, the

xylem exarch, of the root pass into collaterally placed bundles containing both xylem and phloem, the xylem usually endarch. The change from one type of vascular structure to the other takes place in a part of the axis called the *transition region*. The changes occur either abruptly or gradually, the length of the transition region, which is commonly short, varying from less than a millimeter to 2 or 3, rarely several centimeters. The transition may occur in the top of the radicle, at the very base of the hypocotyl, near its center, or in the upper part. Thus the hypocotyl may possess root structure or stem structure through most of its length, or may be largely given over to transition region. Often the transition region coincides with that of the origin of the traces to the cotyledons, ending with the cotyledonary node; as a result of this condition, the structure of the region may be further complicated. Whenever the inversion of the bundles has not been accomplished at the level at which the traces depart, these outgoing strands are inverted during their passage into the cotyledons. In rare cases the transition region extends to the first or even third or fourth nodes above the cotyledons; a portion of the stem then possesses bundles which are partly inverted. In the monocotyledons and the pteridophytes the region is very short.

Externally, this limiting region of root and stem is sometimes visible as a line of depression, or of change in diameter. In many plants, however, such an external line does not correspond exactly with the transition region.

In the change from root to stem there is commonly a considerable increase in the diameter of the stele. Accompanying this go multiplication of vascular tissues and a forking, rotation, and fusion of strands. These changes take place according to a definite plan, of which four somewhat different types have been recognized.

Type a. (Fig. 111, A).—Each xylem strand of the root forks by radial division; the branches, as they pass upward, swing laterally, one to the right and one to the left, turning at the same time through 180 degrees, and join the phloem strands on the inside. The latter have meanwhile remained unchanged in position and orientation, passing as straight strands from the root into the stem. In this type there are formed in the stem as many primary bundles as there are phloem strands in the root. Examples of plants in which this type occurs are *Dipsacus*, *Mirabilis*, and *Fumaria*.

Type b. (Fig. 111, B).—This type differs from the first type in that the strands of phloem, as well as those of xylem, fork, the branches of each swinging laterally as they pass upward to meet in pairs in positions alternating with those of the strands in the root. The xylem strands become inverted as before; the phloem strands retain their orientation. There are thus formed in the stem twice as many bundles as there are phloem strands in the root. This type of transition is more common

than the first. It occurs, for instance, in *Acer*, *Cucurbita*, *Phaseolus*, and *Tropaeolum*.

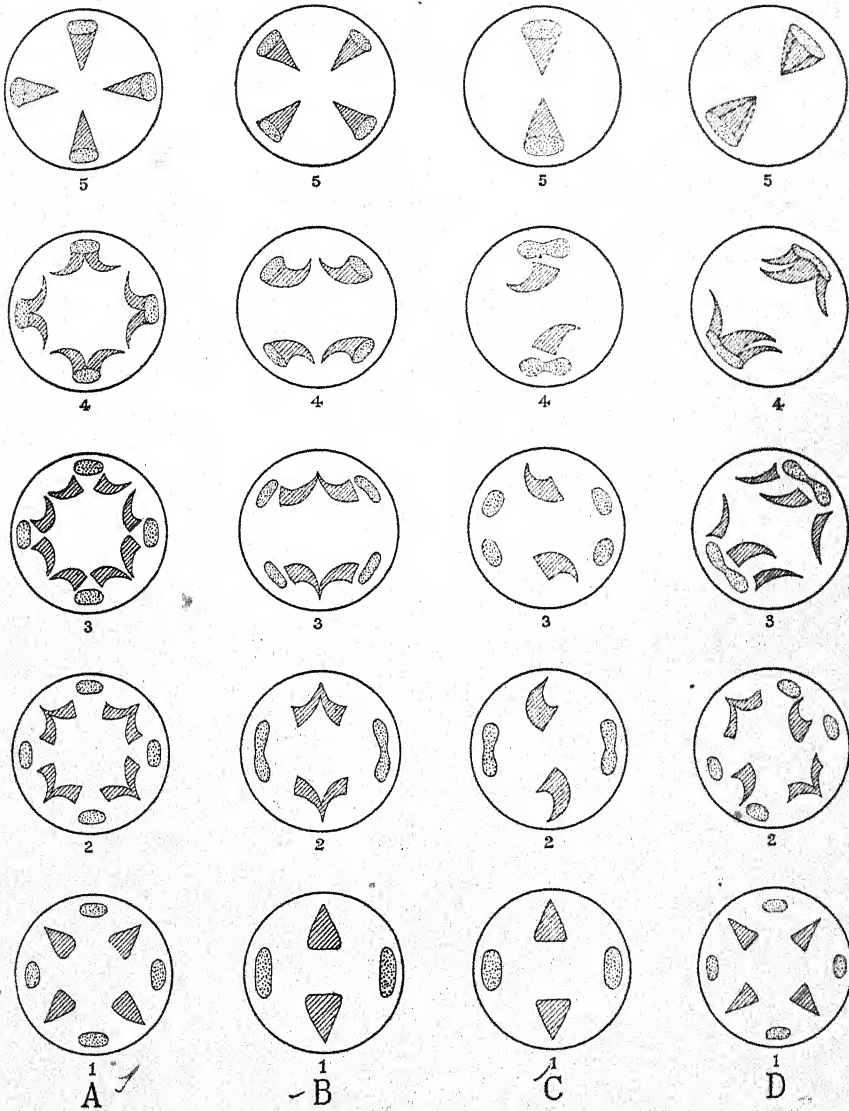


FIG. 111.—Root-stem transition; diagram of four types, A, B, C, D (see text). Figures A-1, B-1, etc., root; A-5, B-5, etc., stem; intermediate figures represent stages in transition found at successive levels, showing splitting, rotation, and fusion of the vascular strands. Xylem cross-hatched; phloem stippled.

Type c. (Fig. 111, C).—In the third type, the xylem strands do not divide, but continue their direct course into the stem, twisting, however,

through 180 degrees. The phloem strands meanwhile divide, and the halves swing laterally to the position of the xylem, joining the xylem strands on the outside. In this type, as in the first, as many bundles are formed in the stem as there are phloem strands in the root. Examples of plants in which this type occurs are *Medicago*, *Lathyrus*, and *Phoenix*.

Type d. (Fig. 111, D).—In the fourth type, half of the xylem strands divide and the branches swing laterally to join the other unforking strands, which meanwhile become inverted. The phloem strands do not divide, but unite in pairs with the triple strands. Thus a bundle of the stem is made up of five united strands, and there are but half as many bundles in the stem as there are phloem strands in the root. This type of transition is rare, and apparently is known only in a few monocotyledons, such as *Anemarrhena*.

Where internal phloem is present in the stem, branches depart from the phloem strands of the root at the level at which the root structure begins to change. These branches pass inward and come to lie inside the new xylem strands, establishing bicollateral bundles. Where the xylem strands of the root are united laterally to form a hollow cylinder (a pith is probably always present in the very top of the seedling root adjacent to the transition region), the strands become separated before the forking or the change in position and orientation occurs.

In some of the monocotyledons the transition region is very short and its structure difficult of determination, owing to the development of a ring of vascular tissue in connection with the attachment of numerous strong lateral roots which develop at that point. In the cycads, the transition region contains a plate or a ring of vascular tissue into which all the strands of the stem and root pass. In these plants the bundles of the stem and root do not, therefore, pass directly into one another.

TYPES OF STEMS

The fundamental structure of stems has already been discussed (Chap. V). In review, it may be said that stems are commonly siphonostelic—protosteles occurring in living plants only among the ferns and some other pteridophytes—and in the majority of cases possess secondary growth. Stems differ greatly in the amount and arrangement of primary vascular tissue and in the amount of secondary tissues. The primary vascular tissue ranges in amount from that in a complete cylinder of considerable thickness to that of a few small strands forming isolated bundles. The various conditions apparently represent stages in evolutionary progress where there has been a thinning of the cylinder of primary vascular tissue, a breaking up of the cylinder into longitudinal strands, and changes in the arrangement of the resulting bundles so that these no longer form a cylindrical series. Whatever the amount and the arrangement of the primary xylem, the secondary vascular tissues may form a solid cylinder

enclosing it and thus develop an unbroken vascular cylinder even from a series of irregularly placed strands. The amount and the arrangement of secondary xylem also vary from that of the complete cylinder of indefinite thickness formed in typical perennial woody axes to the isolated thin strands of certain types of annual herbaceous stems, and to the condition in other plants where secondary growth is absent. Secondary vascular tissues, like primary, have been reduced in evolutionary modification, the cylinder being first thinned radially, and then broken up tangentially. In forms most specialized in this respect, no secondary vascular tissues are formed. All stages in these changes in primary and secondary vascular tissues are represented among living plants. Thus, great variety is to be found in stem structure.

The Woody Stem.—The stems of perennial woody plants present one of the simplest types of stem structure. In these, a more or less continuous cylinder of primary xylem is ensheathed by an unbroken cylinder of secondary xylem which is added to indefinitely. The primary cylinder of this type of stem may be unbroken (save for leaf and branch gaps), as in *Pinus* and *Liquidambar* (Fig. 112, A), or may consist of strands separated rather widely, as in *Platanus*, (Fig. 112, B), and in many shrubs, such as *Berberis*. In all cases the primary cylinder is thin and the primary xylem merges into the secondary xylem so that often only an approximate line between the two can be determined.

The Herbaceous Stem.—The annual stems of plants are often supposed to have their vascular tissues characteristically in the form of bundles arranged in a cylinder (Fig. 112, F). This condition is, however, not typical of herbaceous plants. Among dicotyledons the majority of herbaceous forms possess cylinders of vascular tissue that are complete, except for the presence of leaf and branch gaps (Fig. 112, E). Such conditions obtain not only in coarse and stout stems, such as those of many composites, mints, and legumes, but even in slender delicate stems, such as those of species of *Veronica* and *Stellaria*. The herbaceous stem with discrete bundles is, therefore, not to be thought of as typical of annual stems. It represents, clearly, the extreme stage of reduction of vascular tissues. Though infrequent in occurrence, it is to be found in various families and in both stout and slender plants. In some forms, for example, in species of *Trifolium*, *Geum*, and *Agrimonia*, the lower part of the stem may have a complete cylinder of vascular tissue, and the upper part separate bundles. The condition in monocotyledons is essentially the same as that in extreme dicotyledonous herbs; here the bundles may lie in a ring, but more frequently they are distributed through the stele according to a plan determined by the number of leaf traces, leaf arrangement, and other factors (Fig. 113).

Structurally, herbaceous stems are essentially similar to woody stems; the differences are quantitative rather than qualitative. Distinction

between the types must be based chiefly on period of persistence. And even this is invalid, since in warm climates herbaceous stems may persist more than one year and may even become "woody," and typical woody stems may become annual under some climatic conditions. The herbaceous stem is one in which cambium growth has become limited to

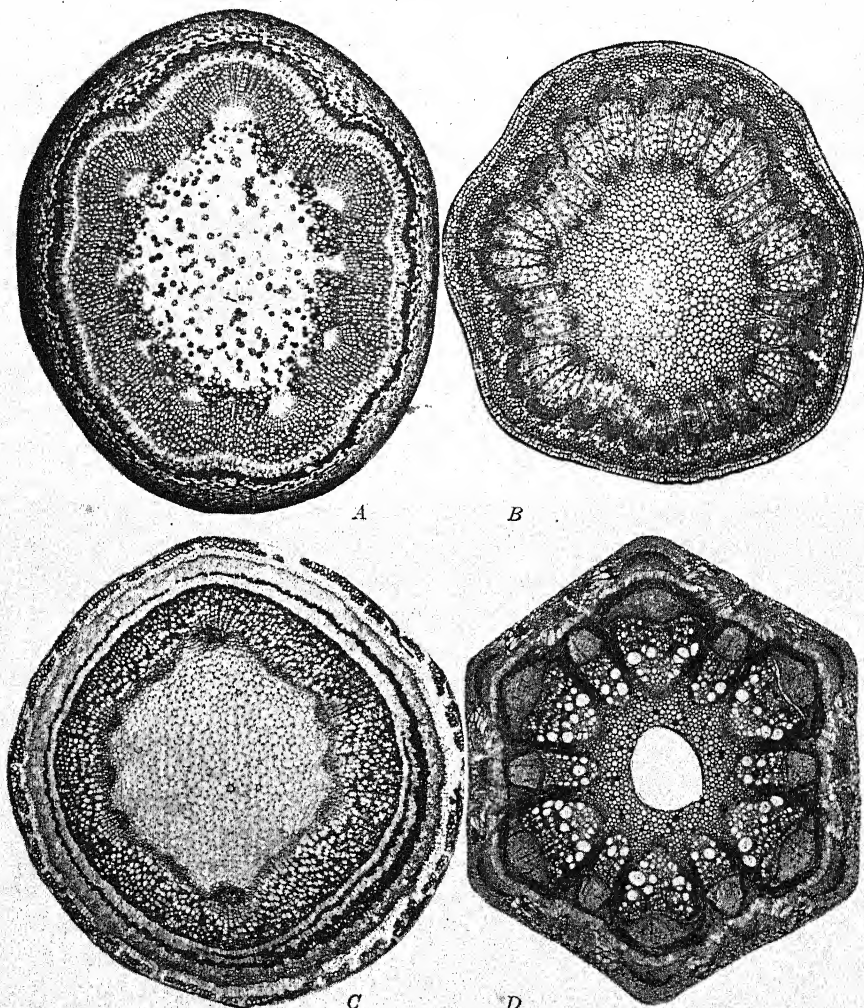


FIG. 112.—Types of dicotyledonous stems. A, *Liquidambar*, tree, stele continuous. B, *Platanus*, tree, stele dissected. C, *Lonicera*, woody vine, stele continuous. D, *Clematis*, woody vine, stele dissected. (Fig. continued on opposite page.)

one season, or part of one season, or is lacking, and where the vascular tissues, both primary and secondary, are in many cases greatly reduced. Woody stems, such as those of some palms and other monocotyledons, may, of course, be developed without secondary growth. The type of

herbaceous stem formed depends upon the type of stele present in the woody ancestral forms. Where the vascular cylinder of the woody type possesses primary tissues in the form of a continuous cylinder, related

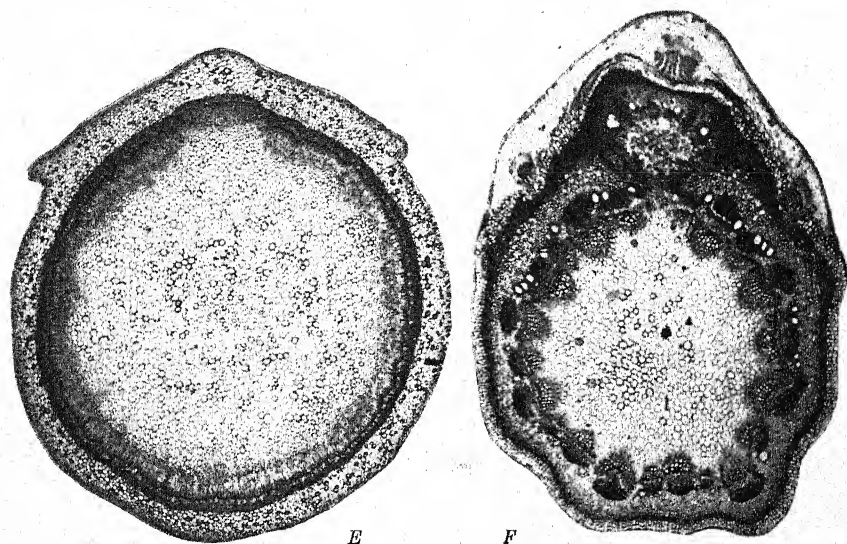


FIG. 112 (continued from opposite page).—Types of dicotyledonous stems. *E*, *Digitalis*, herb, stele continuous. *F*, *Artemisia*, herb, stele dissected. (After Sinnott and Bailey.)

herbaceous forms also possess unbroken primary cylinders; where the primary cylinder of woody forms is discontinuous, owing to the presence of wide, multiseriate rays, related herbaceous plants have a type of stele in which the cylinder consists of discrete bundles.

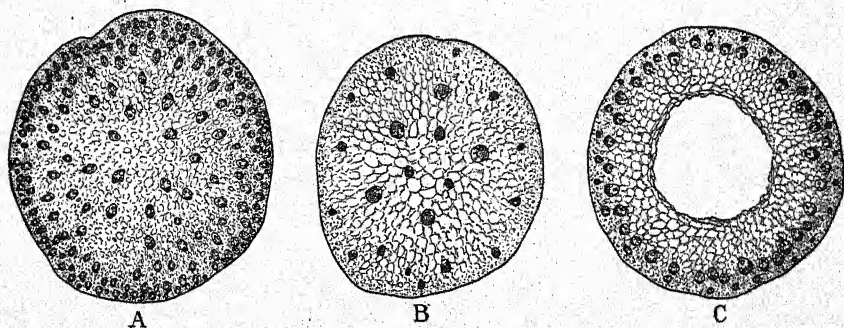


FIG. 113.—Diagrams of monocotyledonous stems. *A*, *Zea Mays*, many bundles, no pith cavity. *B*, *Trillium grandiflorum*, few scattered bundles. *C*, *Triticum sativum*, many bundles about the periphery, central pith cavity.

The question of the morphological features underlying the evolutionary change from the woody to the herbaceous stem, and of the factors determining and controlling the structural change, does not fall within

the scope of this textbook. It seems to have been clearly shown, however, from the evidence of comparative morphology and of the fossil record, that the herbaceous type of stem has been derived from the woody, and not the woody from the herbaceous. The woody type of cylinder is the primitive type; from it by reduction has been derived the herbaceous type.

The Monocotyledonous Stem.—Secondary growth of the usual type is typically lacking throughout the body of monocotyledons. Vestiges of cambial activity in the bundles both of the stem and the leaves have, however, been found in nearly all groups, as, for example, the grasses, sedges, and lilies. The stele is broken up into bundles which are distributed throughout the axis; the endodermis is lacking, and the limit of cortex, pericycle, and pith are often indistinguishable, since bundles are scattered throughout (Fig. 113, A, B). In many forms, however, as in most grasses, there is present a central region (Figs. 113, C; 137, A)—which may or may not represent the pith morphologically—in which no bundles occur; in many forms a more or less readily separable cortical region may also be seen.

The vascular system of most monocotyledons is very complex. The leaf-trace bundles are numerous and follow various types of courses in their descent, uniting in different ways with other strands (Fig. 60, E-M). A common condition is as follows: all bundles are common bundles. The traces, upon entering the stem from the leaf, penetrate deeply, the median traces more deeply than the lateral, and then in their descent return toward the periphery. The downward course may be vertical, or the traces may swing laterally and become oriented in various ways. Each common bundle sooner or later fuses with other similar bundles. The anastomoses occur chiefly at the nodes, and in some groups, such as the grasses, are very abundant and almost restricted to that region.

Secondary Growth in Monocotyledons.—Though typical secondary thickening is lacking in monocotyledons, some of the more woody forms of the group possess secondary increase in diameter of a somewhat similar nature. This increase is accomplished by the formation of a cambium in the innermost cortex or in the pericycle. Such a cambium differs from the typical cambium in that the cells composing it, though vertically elongated, are short and rectangular, the ends of the cells not tapering. It further differs from a normal cambium in that the tissues formed by it are almost entirely toward the center of the stem, and these constitute not a uniform tissue but a system of vascular bundles embedded in parenchyma (Fig. 78).

The bundles are usually without definite order of arrangement, though they may lie to some extent in radial rows. Occasional anastomoses occur. The bundles are collateral, or, more frequently, amphivasal, the phloem being of small amount, and the xylem often largely of

fiber tracheids or fibers. The interfascicular parenchyma in most cases shows marked radial arrangement due to its mode of origin. Each cell of this tissue is similar in shape to the cambium cell from which it was derived; the cells of the vascular bundles, however, are much longer and have tapering ends. In the development of these cells from the cambium, a considerable number of divisions takes place in a small group of mother cells formed by the cambium. These divisions are longitudinal and at first largely in the tangential and radial planes; later, they may occur in any plane (Fig. 114). Rapid elongation and extensive gliding growth follow. The ontogeny of these secondary bundles closely resembles that of the primary bundles, especially in the procambial stages.

The scanty cells formed toward the cortex are parenchymatous, and often separable only with difficulty from the primary cortical cells.

Secondary growth of this type is indefinite in amount, as is that of the normal type. It is, however, usually of slow development, and large trunks are not commonly formed. There is usually no evidence of annual-ring demarcation, but in a few cases (*Aloë*) weakly defined annual bands occur.

Increase in diameter of this type occurs in the arborescent Liliiflorae, for example, *Dracaena*, *Yucca*, *Aloë*, *Cordylina*, and in fleshy parts of some of the Dioscoreae. It has been reported in a few cases among the palms, but in nearly all of these tree-like monocotyledons the growth is entirely primary.

The Vine Type of Stem.—The stems of vines are of both structural types, many vines, such as *Vitis*, *Celastrus*, and *Solanum Dulcamara*, possess woody steles (Fig. 112, C); others, such as *Clematis* and *Humulus*, have their vascular tissues arranged in the form of a ring of bundles (Fig. 112, D). These bundles are separated by rays of parenchyma, which in many forms are increased, like the bundles, by cambial growth. In such forms, as in the type of herbaceous stem with separated bundles, the xylem and phloem are highly specialized in structure. Vascular

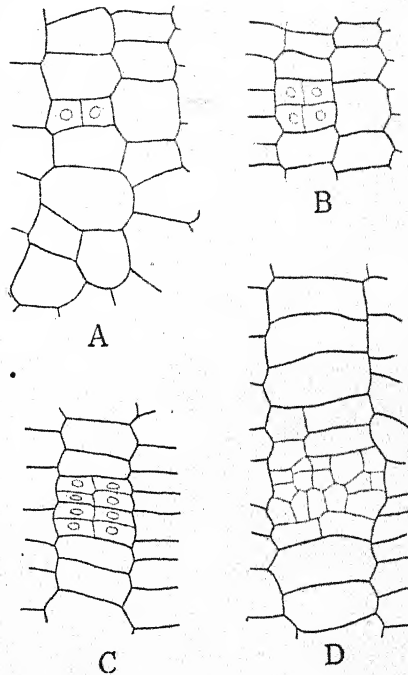


FIG. 114.—Diagrams illustrating early development of bundle in secondary growth of monocotyledons; *Aloë pleuridens*. A-D, successive stages. (After Chamberlain.)

rays are commonly absent, the vessels are porous and of large diameter, tracheids and fibers are proportionately few, sieve tubes are of the highest type, and phloem parenchyma and fibers are scarce or lacking. Many vines show not merely these tissue specializations, but also possess anomalous general structure. In this group fall *Aristolochia* and *Menispermum*, which, unfortunately, are often cited as examples of typical stem structure, and used to demonstrate the origin of a woody from an herbaceous stem. The structure of anomalous stems is discussed on p. 256.

In the stem of the young herbaceous vine, such as that of *Pisum*, *Apios*, and *Adlumia*, there is present a circle of vascular bundles separated by rather wide segments of parenchyma. Such is also the structure of some rather woody vines, for example, *Clematis*. In these stems the cambium may be restricted to the bundles, as in *Adlumia*, or may form a complete cylinder by extension across the interfascicular rays of parenchyma. This interfascicular cambium may be vestigial, as in the upper parts of the pea vine, forming no secondary tissue, or a very few vascular cells, as at the base of the pea vine; or it may be very active, increasing the parenchymatous rays at the same rate as the fascicular cambium builds up the bundles, as is the condition in *Clematis*. In such cases as the last, the type of structure found in the one-year stem is maintained as the stem becomes woody and perennial. Yet, since the bundles increase in tangential extent as secondary growth continues, the stem apparently becomes a woody stem. The bundles are, however, still separated, though by wedges of secondary rather than primary parenchyma. These radial plates or rays of tissue extend in most cases from node to node, and constitute an important feature of vine structure. Such rays, either of primary structure, or of both primary and secondary structure, are prominent structural features of many vines, both annual and perennial. They are present also in vines with complete woody cylinders, and constitute one of the prominent modifications of such steles found in lianas (Fig. 118). These parenchymatous segments extend in most cases from node to node, and often for several internodes. Being of soft tissue, they are sometimes crushed as the stem becomes older, perhaps due to the "play" of the bundles upon one another during the periods of lateral stresses to which a vine stem is peculiarly subject. Apparently, this type of structure is the result of one method of adaptation to the mechanical requirements of vines.

The "Medullary Rays" of Vines and Herbs.—In vines and herbs with dissected vascular cylinders, the bundles are in early stages separated by sheets of parenchyma which merge internally with the pith and externally with the cortex (Fig. 112, *D, F*). In these early stages there is usually little or no evidence of limitation of pith or cortex in the region of these bands, nor is there histological evidence that they belong morphologically, even in part, to the vascular cylinder. Since they appear as

radiating portions of the pith, they are commonly called *medullary rays*. When these primary structures are later increased in radial extent by secondary growth, as they are in many vines, such as *Clematis* (Fig. 112, D), they closely resemble broad "medullary rays" (vascular rays) of secondary wood and phloem. Hence it is that both these rays and true vascular rays have been termed "medullary rays," and believed to be identical. The idea that the woody stem is developed from the herbaceous stem is based in large part upon this misconception. It is clear that such broad rays of vines and herbs extend from node to node, and in this respect differ much from the vascular rays which are of very limited vertical extent. Further, they clearly represent, morphologically, entire segments of the vascular cylinder, being equivalent to many vascular rays plus the tissue surrounding and included between these rays. It is obvious that the same term should not be applied to both types of rays. The term "medullary ray" as applied to rays of secondary vascular tissue is inapt, and should be supplanted by the term "vascular ray." Since the rays of vines and herbs are, when only primary, very like projections of the pith, they may perhaps aptly be called medullary rays, especially if this term is not applied to vascular rays. That they are not homologous with the structures known commonly as medullary rays should be kept in mind.

Internal (or Intraxylary) Phloem.—In the siphonosteles of ferns the amphiphloic condition is usually prominent. Here the internal phloem forms a continuous layer and is closely similar to the external phloem. In the angiosperms, where internal phloem is also frequently present, this tissue is less conspicuous. It occurs usually as strands, large or small, more or less definitely associated with the primary xylem (Fig. 115). In amphiphloic ferns, where the cylinder is broken up by leaf gaps, the internal phloem unites with the external through the gaps, and amphicribal bundles are formed (Fig. 116, B). In angiosperms with internal phloem and broken vascular cylinder, the internal phloem forms the innermost part of bicollateral bundles, as in *Cucurbita*; where the primary xylem forms a more or less complete cylinder, strands of internal phloem also form a fairly continuous layer. Internal phloem is in most cases only primary; rarely a cambium arises inside the primary xylem and a small amount of secondary phloem is formed, as in *Tecoma*.

The cells of internal phloem are like those of external phloem, except that fibers are few or lacking, and the sieve tubes and companion cells occur in small, restricted groups, surrounded by parenchyma (Fig. 115). This parenchyma, together with that of the protoxylem region, forms the perimedullary zone (Chap. V) of the pith. Such a layer is, of course, morphologically, a part of the vascular cylinder and not the outer layer of the pith. Where an inner endodermis is present, this layer separates the inner phloem from the pith. The internal phloem and the internal

endodermis are often continuous through leaf and branch gaps with the outer phloem and the outer endodermis.

Internal phloem occurs in many families among the angiosperms, chiefly in the more highly specialized groups, such as the Solanaceae, Gentianaceae, Myrtaceae, Cucurbitaceae, Convolvulaceae, Apocynaceae, Asclepiadaceae, Onagraceae, Campanulaceae, and Compositae. In some of these cases the internal phloem is apparently degenerate; in others it probably plays a prominent part in conduction. The latter is the condition in the tomato and potato plants, especially in the rhizomes and tubers of the potato. In the potato tuber, except for a slender central core, strands of internal phloem are present throughout the region

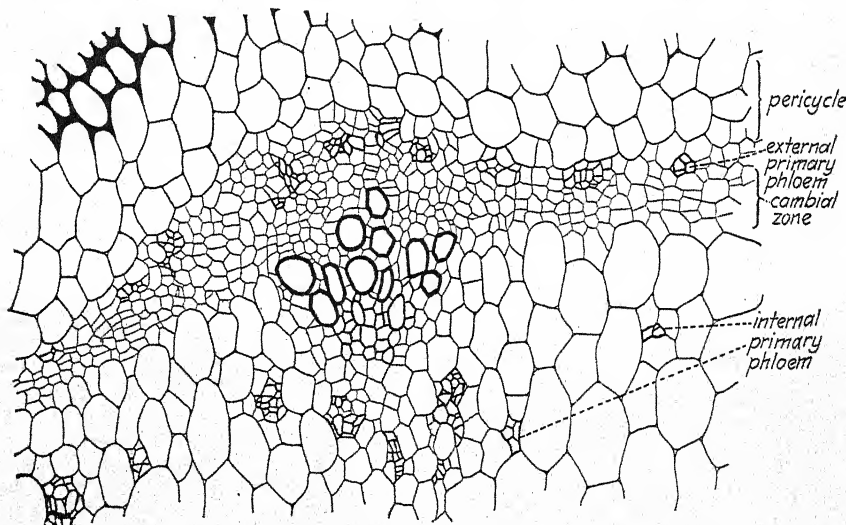


FIG. 115.—Internal (intraxylary) phloem in young stem of *Solanum tuberosum*. The primary phloem cells are in small groups external and internal to the cambial zone. (After Artschwager.)

inside the thin xylem cylinder. Like the pith, the cortex is also narrow. Hence, the storage tissue of the potato is to a large extent a parenchymatous vascular cylinder; the pith makes up but a small part of the tuber.

The Vascular Bundle.¹—The vascular tissues of a plant form a continuous system. In the axes of the majority of plants these tissues are arranged in the form of solid or hollow cylinders. In the axes of many other plants, however, and in appendages generally, the vascular tissues occur in more or less distinct strands, which are united proximally and sometimes also distally with other similar bundles or with the central

¹ A general discussion of the vascular bundle is placed in this chapter for convenience alone. Bundles are not, of course, restricted to stems. Further discussion of bundle structure will be found in other chapters.

vascular tissues. To these more or less free parts or extensions of the vascular body the term *vascular bundle* is applied (p. 95). The bundle

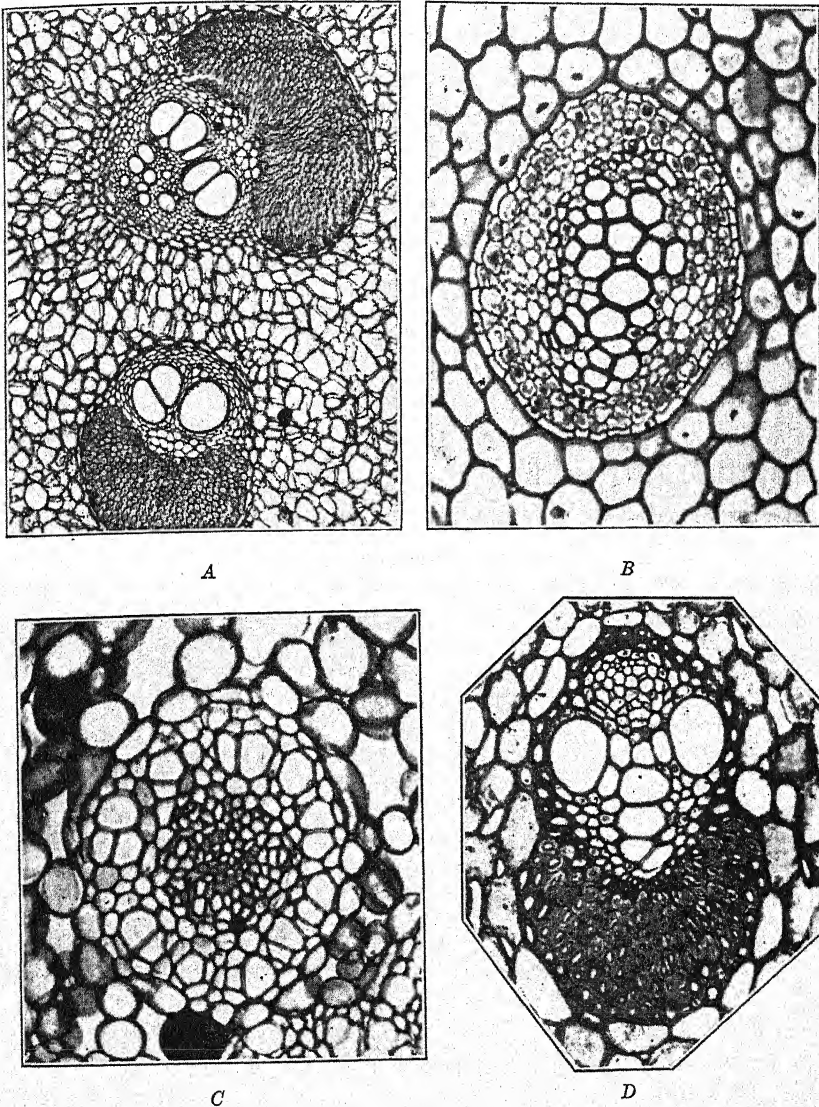


FIG. 116.—Vascular bundles. *A*, *Sabal Palmetto*; collateral monocotyledonous bundles with heavy bundle cap. *B*, *Polypodium vulgare*; amphieribral bundle. *C*, *Acorus Calamus*, amphivasal bundle. *D*, *Scirpus lineatus*; collateral monocotyledonous bundle, with sclerenchyma sheath, two prominent vessels flanking the circular phloem mass.

is, obviously, an important structural feature of the plant; but as such it has doubtless received undue attention. It seems clear from the

study of the stele and of the relationship of axis and appendages that the bundle is merely a more or less segregated portion of the conducting system. In the axis the bundle is apparently not the fundamental unit of structure, from which the vascular cylinder has been built up. The disposition of the tissues in a cylinder seems to be the primitive condition, and the discrete bundles of axes are the portions of such a cylinder broken up in specialization (Chap. V). Certainly the bundle of the stem is best interpreted in this way, both from a morphological and from a histological point of view.

Size and Shape of the Vascular Bundle.—Vascular bundles vary greatly in structure and shape, in course taken in the plant body, and in relation to other bundles and the central vascular body. The various types of bundles, is so far as they depend upon the relationship of xylem and phloem to each other in the bundle (concentric, collateral, etc.), and upon the course of bundles in the axis (cauline and common), have already been considered in Chapters IV and V. Since any essentially free strand of the vascular system, large or small, may be called a bundle, a bundle, as seen in cross section, may consist of an indefinite number of cells, or of very few, even one (Fig. 123). Bundle tips in leaves and fruits often consist of a single cell. In cross-sectional shape, the bundle is most commonly oblong, or elliptical, but linear, forked, and irregularly shaped bundles also occur.

Histological Structure of the Vascular Bundle.—The proportionate amount of xylem and phloem varies much in both collateral and concentric types of bundles. In both types the bundle may consist largely of one tissue, and collateral bundles are in some instances (reduced or vestigial bundles, and bundle tips) made up of xylem or phloem alone. In collateral bundles the xylem, especially when small in amount, may extend laterally about the phloem to a greater or less extent, a condition found in *Equisetum*, in some monocotyledons, and in other herbaceous angiosperms. In such cases the xylem of a bundle may even be separated into groups.

In some specialized bundles the cells of both xylem and phloem are reduced in number, fibers and parenchyma cells being few or lacking in each tissue. Thus the phloem of such bundles may consist wholly of sieve tubes and companion cells, the xylem of vessels and tracheids, or of vessels alone. This is the condition in many monocotyledons, and in some dicotyledons, such as certain genera of the Ranunculaceae. Under these conditions the sieve tubes and companion cells are often symmetrically arranged, and of the few vessels one, two, or three are of large diameter. In the bundle of monocotyledons there are in many forms two huge vessels, one on each "shoulder" of the xylem group, as in *Zea*; in fewer forms there is one very large central vessel, as in *Musa*. In still other genera the vessels are all pretty much alike in size.

Small bundles are, of course, largely or wholly of primary tissues, and therefore commonly have their cells arranged irregularly. In many dicotyledons, however, even the primary vascular tissues are arranged in radial rows, for example, in *Trifolium* (Fig. 117, A) and *Asclepias*. Where the bundle has a small amount of secondary tissues, the central part usually shows weak radial arrangement and the inner and outer cells are irregularly arranged.

Just as the proportion of primary and secondary tissues varies, so does that of protoxylem and metaxylem, the former being commonly

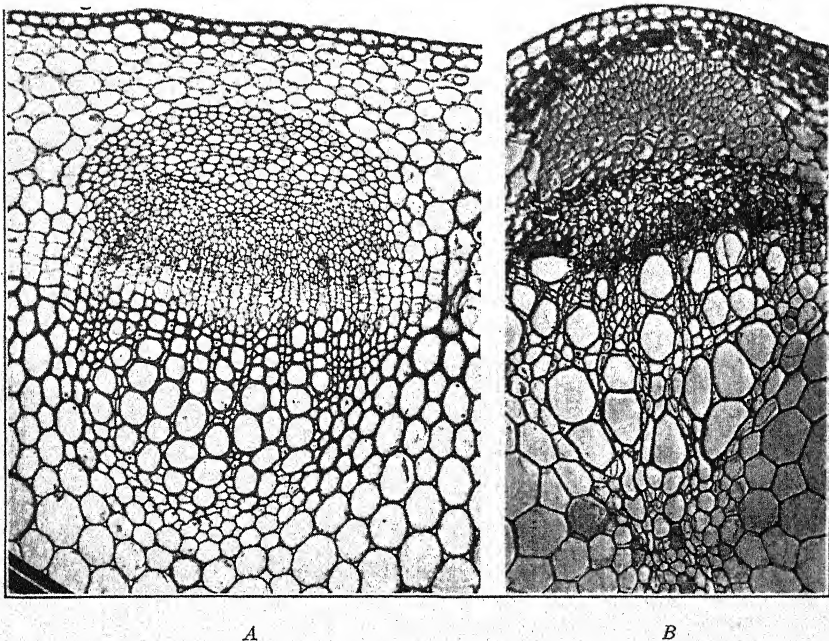


FIG. 117.—Collateral dicotyledonous vascular bundles. A, *Trifolium pratense*; young bundle, secondary growth in early stages, primary xylem radially arranged, bundle cap immature. B, *Pisum sativum*, mature bundle, primary and secondary tissues irregularly arranged.

large in amount in small stem and leaf bundles. The extent to which protoxylem lacunae are formed likewise varies; such spaces are especially large in many of the monocotyledons.

The "Fibrovascular" Bundle.—The vascular bundle is often associated with one or more strands of fibers, a complex conducting and supporting structure being thus formed. This unit has been long—and aptly—called a fibrovascular bundle. Unfortunately, however, this term has been extended to bundles which possessed no fibrous cap or sheath, and has in usage come to be applied to all vascular strands, simple or complex. The strand of xylem and phloem, as a morphological unit, a part of the

vascular system, is better termed "vascular bundle" (p. 95); the vascular bundle together with surrounding fibrous structures may perhaps appropriately be called a "fibrovascular bundle."

The association of fibers morphologically external to the bundle with the vascular tissues is apparently connected with the mechanical relations of support for the organ concerned, and support and protection for the softer conducting cells. The fibrous cells associated with vascular bundles most commonly form "caps" or crescent-shaped masses (in cross section) externally, or both externally and internally, to the bundle (Figs. 112, *D, F*; 116, *A, D*). These caps may be united laterally by flanges of similar cells, so that a complete supporting and protecting cylinder is formed. Such fibers, when external, belong commonly to the pericycle, though they are often wholly or in part cortical. Where the bundles are rather widely separated, and especially in cases where they are much reduced and specialized, they are often completely ensheathed by fibers (Fig. 116, *D*). This is the condition in the stems of many monocotyledons and other herbaceous forms.

The term "vascular bundle" is used in studies of physiological anatomy to denote bundles without fibrous sheaths, in which the xylem and phloem themselves contain no fibers. In the physiological sense the term "fibrovascular bundle" indicates a bundle whose xylem and phloem contain fibers as a constituent part of these tissues, whether or not fibers external to these conducting tissues are also present.

ANOMALOUS STRUCTURE IN STEMS

Though the great majority of plants possess stelar structure of the type considered normal, many are known to have unusual structure. This structure is of many different types, which, however, fall into two groups: (1) those in which a cambium of normal type and persistence, by peculiarity or irregularity in its activity, develops vascular tissues of unusual arrangement and proportion of xylem and phloem; (2) those in which the cambium, and, consequently, the secondary xylem and phloem, are abnormally arranged, or in which the original cambium is replaced by other cambium layers secondarily formed. These additional layers may also be of unusual extent and arrangement. To the many combinations of unusual structure that may be produced by these modifications may be added the anomaly of the presence of medullary and cortical bundles. As a result, extremely complex structural conditions may be found. The interpretation of all such conditions may usually readily be made by ontogenetic studies, either of the developing axis itself or of the seedling. Descriptions of a few of the many varieties of anomalous structure will give an idea of the principal types of departure from the normal.

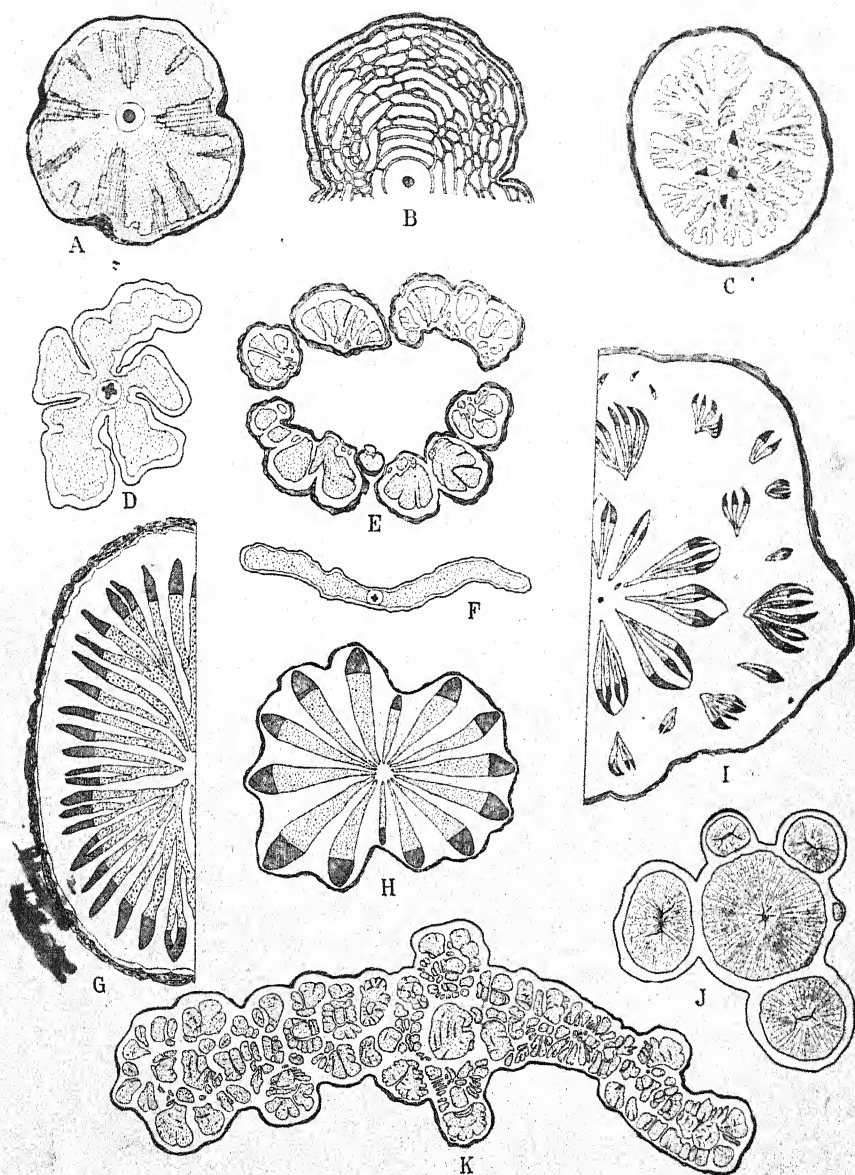


FIG. 118.—Anomalous stem structure—liana types. A, Bignoniaceous genus. B, *Securidaca lanceolata*. C, *Bignonia* sp. D, *Bauhinia rubiginosa*. E, *Serjania ichthyocarpa*. F, *Bauhinia* sp. G, *Aristolochia triangularis*. H, *Begonia fruticosa*. I, *Piper Aluminense*. J, *Thinosia scandens*. K, *Bauhinia Langsdorffiana*. (After Schenck.)

Where a cambium, normal in position and activity, forms in some of its segments much larger proportions of xylem than of phloem, and in others more phloem than xylem, a ridged and furrowed xylem cylinder is formed. This may be of simple structure, as in Fig. 118, A, or very complex, as in Fig. 118, C. In certain cases, as in *Aristolochia* (Fig. 118, G), segments of the cambium form only ray-like parenchyma, new areas of cambium constantly being given to the formation of rays of parenchyma. A strongly fluted vascular cylinder is thus formed. Restriction of the activity of the cambium to certain regions may also result in the formation of ridged stems (Fig. 118, D). Strap-like stems (Fig. 118, F) may be formed in the same manner.

Stems of other peculiar shapes or types are formed by the unusual position of the cambium, this layer, while the stem is young, being thrown into folds or ridges, the tips of which become pinched off, and after separation develop "steles" by themselves (Fig. 118, J). In some plants the cambium probably appears originally in several separated sections, each of which surrounds portions, even individual strands, of the primary vascular tissue. In such cases the stem appears as though made up of several fused stems. This apparently compound condition becomes more marked as the stem becomes older, and the parts separate as the outer layers of each strand die because of the development of periderm layers (Fig. 118, E). There is thus formed a stem composed of strands lying together more or less like the strands of a rope. A somewhat similar condition is brought about by the breaking into strips of the original cambium cylinder, and even of the vascular cylinder formed by this meristem, by the proliferation of xylem parenchyma (Fig. 118, K). Excessive increase of parenchyma in the xylem and phloem ruptures the first-formed, original tissues and the cambium sheet which formed them.

Interxylary Phloem.—Variations of another type in the activity of the cambium produce *interxylary phloem*. Phloem of this type is secondary phloem in the form of strands embedded in secondary xylem. There appear to be two methods by which interxylary phloem comes to lie embedded in secondary xylem. It is possible, however, that only one method (the second described below) obtains in all cases, since behavior of the cambium in such growth types has been studied in detail in but few instances. In genera like *Combretum* and *Entada*, small segments of the cambium are said to produce phloem cells toward the inside for a brief period, in place of the xylem cells which are normally produced. After a brief period of such activity these cambium segments return to normal function, and thus bury the inwardly formed phloem with xylem. In other forms, such as *Strychnos*, the interxylary phloem strands are formed by the cambium toward the outside as a part of the normal external phloem, but the strands later become embedded in the xylem in the following manner. Small segments of the cambium cease to function,

their cells becoming transformed into mature conducting tissue. New segments of cambium then arise, as secondary meristems, in the phloem some few rows of cells out from the original cambium, or in the pericycle. These unite with the edges of the segments of the general cambium cylinder—which have continued meanwhile their normal activity—and thus enclose a strand of phloem cells. This is repeated in other segments of the cambium so that the secondary xylem possesses numerous scattered strands of embedded phloem.

The formation of phloem embedded in other secondary tissues occurs also, of course, in secondary growth in monocotyledons (p. 248). Here, however, the development of the conducting tissues from cells formed by the cambium is similar to the development of primary bundles. Other types of phloem burial are brought about by the development of accessory cambium layers external to the phloem, as discussed in the following paragraphs. In some genera, a combination of these methods occurs.

Accessory Cambium Formation and Activity.—The formation of secondary cambial zones is responsible for many of the unusual types of stems. These meristems commonly develop in the pericycle and function as does a normal cambium, or, in case the first cambium has functioned in an unusual manner, repeat this peculiar behavior. Such secondary cambial activity follows the cessation of function of the first layer, one or even many additional layers successively appearing and ceasing to function. Thus a cylinder of alternate concentric layers of xylem and phloem is formed (Fig. 118, B). The restriction of the extent of the secondary cambium layers to certain narrow parts of the circumference results in the formation of much ridged or flattened stems, and, where the secondary layers form on but one side, or on two opposite sides, of a strap-like stem (Fig. 118, F).

Of these types of modified stele, the majority are found in plants of special growth habit, very many of them lianas; the modifications appear to be largely associated with the habit of the stem and with the mechanical demands upon its structure.

In the Chenopodiaceae, Amaranthaceae, and allied families a somewhat different type of unusual growth is present. Here there is first formed a hollow cylinder of vascular tissue or a ring of irregularly arranged bundles. These bundles are partly of secondary nature, but cambial activity soon ceases and a new, secondary cambium arises in the pericycle just outside the bundles. In some forms the cambium forms tissues centripetally, consisting of bundles (similar to those already formed) embedded in non-vascular tissue. This embedding tissue, which has been variously termed *conjunctive tissue*, *interfascicular tissue*, and *intermediate tissue*, consists of elongate, lignified cells, which in some shrubby forms make a very hard "wood." Centrifugally, the cambium

forms a very little parenchyma or no cells at all. The "bundles" formed in this way may be arranged irregularly or in definite concentric rings. In some cases, as in *Chenopodium* (Fig. 119), the phloem is formed centrifugally and later buried by the development of an arc of new cambium formed without it (p. 258). In some forms this secondary cambium is said to persist, continuing indefinitely to form this complex tissue of embedded bundles; in other cases, and especially in roots, this first secondary cambium is quickly replaced by others, which in succession form rings of embedded bundles.

The activity of the secondary cambium layers in other members of this group of families is more nearly like that of the normal cambium.

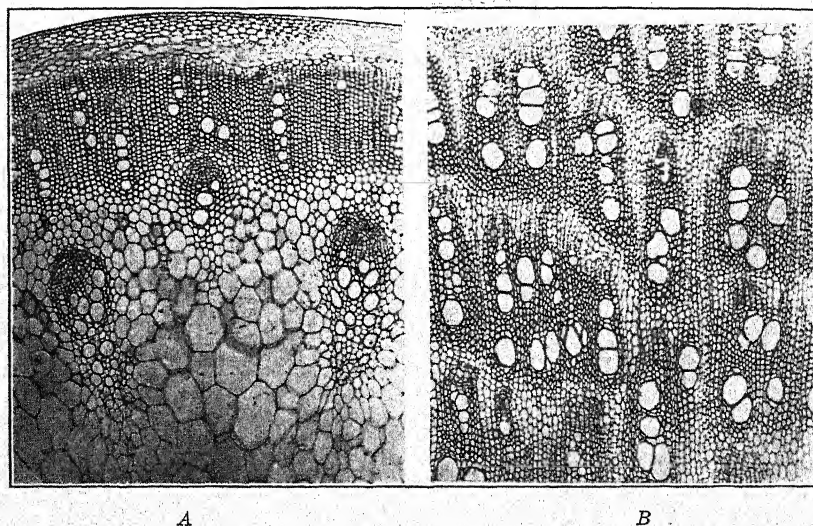


FIG. 119.—Anomalous secondary growth; *Chenopodium album*. A, portion of young stem, showing "medullary" bundles (with primary and secondary tissues), within the secondary cylinder. B, portion of secondary cylinder; alternate bands of xylem, phloem, and "conjunctive tissue," the xylem dark, the phloem in restricted patches, other tissue light.

It is, however, complicated by prolonged primary growth. The development of the common beet root (*Beta vulgaris*) will serve as an example of this type (Fig. 120). The first cambium forms a ring of bundles close about the primary xylem. A secondary cambium soon arises in the pericycle and this is followed in rapid succession by others originating similarly. All layers continue to function, perhaps indefinitely, though more slowly after an early period of activity. The cambium arises apparently as a continuous band, but forms more or less separate bundles, bands of conjunctive parenchyma developing between the vascular strips. The position of each new cambium, as it arises in the pericycle, is such that it encloses a few layers of pericyclic cells. These

rapidly multiply and build up a parenchymatous layer as rapidly, or even more rapidly, than the cambium builds up the vascular layer. Alternate bands of proliferated pericycle and of vascular bundles are thus formed. The former constitute the dark-colored, the latter the light-colored, rings in the beet root. The bundles are themselves largely parenchymatous, but few lignified cells occurring in the xylem. Growth continues through all layers, in the bundles apparently both by cambial activity and by proliferation of the parenchyma of the xylem and the phloem. Thus the beet root increases in diameter by growth throughout its layers. The layers are not in most cases simple cylinders but are united irregularly with other layers, so that a complex, asymmetrical structure is formed.

Anomalous structure is not infrequently due to the presence of medullary and cortical bundles. Such bundles may occur together with other structural peculiarities, or in stems otherwise typical in structure. Medullary bundles are not infrequent in ferns, as in *Pteris*.¹ In the dicotyledons, medullary bundles occur in a considerable number of families, such as the Piperaceae, Ranunculaceae, Amaranthaceae, Berberidaceae, Cucurbitaceae. Cortical bundles are of less frequent occurrence; they are known in the Calycanthaceae and Melastomaceae, rarely elsewhere. Many so-called cortical bundles are leaf-trace bundles which run downward through the cortex for some distance before entering the stele. This is the condition in *Begonia* and *Casuarina*. In plants with a fleshy cortex, such as many of the Cactaceae, where the leaves are reduced and photosynthesis is carried on largely by the cortex, branches from the base of the leaf traces penetrate the cortical tissues.

The various types of stem and root structure which are commonly described as "anomalous" occur in very many families of vascular plants—ferns, gymnosperms (cycads), and angiosperms. In the latter

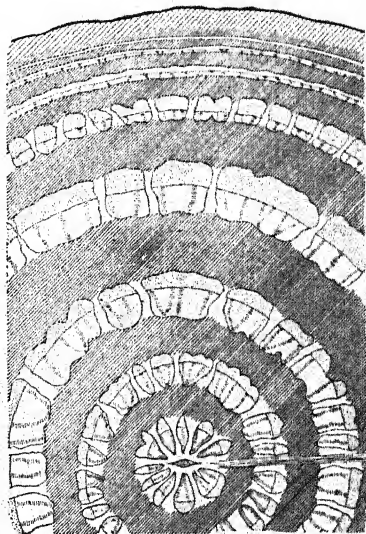


FIG. 120.—Anomalous secondary growth; *Beta vulgaris*, root, cross section. Alternate layers of vascular bundles and proliferated pericycle (cross-hatched); phloem stippled, lignified xylem cells in radial rows, xylem parenchyma and secondary interfascicular tissue unshaded; all layers growing.

¹This fern, so commonly used to illustrate stem structure, is, because of this and other features of unusual structure, an unfortunate choice. It should be supplanted by typical forms.

group, they occur in many families, in some of which all forms are of peculiar structure, in others only a part.

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CHAPTER XII

THE LEAF

Physiologically considered, the leaf is the organ of the plant which is specially adapted to the all-important function of photosynthesis. In a sense, this is the most important of plant functions, since practically all other functions depend upon it or contribute to it either directly or indirectly. Thus the structures having to do with absorption and conduction are important chiefly because they supply the leaf with materials needed in photosynthesis and remove the products formed in this process. The complex mechanical systems of the larger plants are for the most part adaptations to the support of large leaf areas in such relation to light that photosynthesis can go on advantageously. Upon the products of photosynthesis all forms of life, with the exception of a few specialized bacteria, depend directly or indirectly for their food supply. The leaf is thus an exceedingly important organ.

The Leaf as an Expansion of the Axis.—From the standpoint of anatomy, the leaf is a lateral expansion of the axis in which all parts are included. Thus in the leaf, tissues of all parts of the axis—epidermal, cortical, and stelar—are to be found; these are arranged in various ways, the arrangement being chiefly the result of adaptation to the support, protection, and vascular supply of the photosynthetic tissue. The stelar tissues, xylem and phloem, together with accompanying sclerenchyma, form the skeleton upon which the green tissues, which represent the cortex, are supported. The epidermis covers the entire structure, and is continuous with the epidermis of the stem.

The Vascular Skeleton of Leaves.—Leaves consist typically of three parts: the expanded portion, or blade, where most of the green tissue is located; the petiole, which supports the blade on the axis and functions also in conduction; and the stipules. Stipules in many plants are wanting altogether, or are soon lost by abscission, but in some plants are persistent structures which may form an appreciable part of the photosynthetic system, for example, in *Pisum*. The morphological nature of stipules has been much in dispute.

Dependent upon the gross vascular structure, leaves are classed as *parallel veined* when the main bundles traverse the leaf without anastomosis, and *net veined* when the main branches of the vascular system form a network. Pinnate and palmate, closed and open venation, and other

familiar morphological classifications are also based upon the arrangement of the vascular bundles.

"Vein" Islets."—Whatever may be the arrangement of the larger vascular bundles, the ultimate divisions of the conducting strands completely or partly encircle minute areas of the photosynthetic tissue with which they are in close contact (Fig. 121, B, C). These divisions of green tissue have been called *vein islets*, and in a way represent more or less well-defined photosynthetic units. The vascular bundles surrounding the vein islets are in intimate contact physiologically with the photosynthetic tissue in that they lack the sclerenchyma normally present about the larger bundles. The size and the shape of the vein islets vary with different types of venation and with different species; in some cases

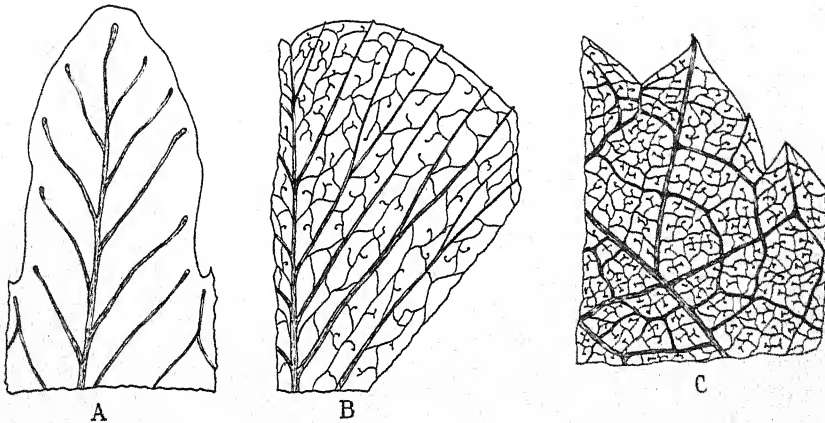


FIG. 121.—Vascular skeleton of leaves. A, pinnule of *Aspidium*; no definite vein islets exist. B, part of leaflet of *Trifolium*; vein islets rather indefinite. C, part of leaf of *Pyrus Malus*; small, definite islets, a frequent type.

definite islets do not exist. As the leaf matures, the islets increase in size, their growth being a part of the general growth throughout the leaf. In full-grown leaves the size of vein islets is apparently constant, regardless of the size of the leaf. It is probable that the size of the islets bears little or no relation to the age of the individual.

The Arrangement of Leaves.—The different types of leaf arrangement on the stem, or phyllotaxy, and the many variations of size and shape which occur are doubtless in part adaptations to the exposure of the photosynthetic surface to light. These variations, although of interest chiefly to taxonomic morphology, are naturally closely bound up with variations in the structure of the plant. Different types of phyllotaxy thus depend upon, or are related to, different arrangements of the leaf traces in the primary vascular cylinder of the plant; and different shapes and sizes of leaf blade are related to suitable variations in the arrangement and

amount of sclerenchyma necessary for support, and of vascular tissues necessary for conduction.

The Ontogeny of the Leaf.—Leaves have their origin in the promeristem of the growing point of the axis as lateral projections of that meristem (Fig. 27). The initiating cells of these lateral structures arise close to the apex of the stem from cells which are in most cases several cell generations removed from the initials in the main axis. By their division these cells form the meristematic protuberance which later develops into the leaf. In some cases only the outermost layer of the meristem, dermatogen or dermatogen-like, takes part in leaf development, but more often cells of the deeper layers are also involved. In these projections of meristematic tissue an apical growing point is early formed, and this by its activity increases the organ in length for a time and lays down its fundamental structure. Such apical growth in leaves is in most plants of comparatively short duration. The apical growing point of fern leaves, however, persists for some time, the leaf tip continuing to develop after the base is mature, even, it is reported, in some cases for more than one year. Commonly, however, apical growth ceases early and general growth throughout the young leaf continues. The general outline and the fundamental structure of most leaves are thus developed while the leaf is yet minute. In the winter buds of temperate-zone trees small leaves are often present, in shape resembling full-grown leaves, with the main vascular structure outlined and a considerable part of the cells already present. Later growth consists to a large extent of the rapid increase in cell size and the maturation of the mesophyll cells and vascular tissues, which takes place during the period of leaf expansion. New cells may be formed generally throughout the leaf during this period. After the leaf attains full size, the larger vascular bundles usually increase in diameter, secondary growth being of frequent occurrence. There is, naturally, great difference in the time taken for leaf development in different plants. In most woody plants of the temperate zone, complete expansion and maturity are attained rapidly. In many tropical plants and in herbaceous forms with very large leaves, development goes on over a longer period. Intercalary leaf meristems are common in leaves of the linear type, occurring in the grasses generally, and in such genera as *Iris*, *Allium*, and *Pinus*. But such meristems also persist for but a comparatively short time, with the exception perhaps of those of the anomalous gymnosperm, *Welwitschia*, where they are apparently unlimited in time of activity.

The Development of Vascular Tissue in the Leaf.—The primary vascular tissues of the leaf blade and petiole form a system continuous with the leaf trace with which they are joined. All parts of this system differentiate from procambium in the same manner, though the time of maturity differs in the different sections. Ordinarily, the first vascular

tissue of the leaf system to mature is the median portion of the leaf trace. Here vascular tissue often matures soon after the formation of the leaf primordium near the growing tip, and from this point the bundle matures progressively in both directions. As the internode elongates, the downward extension of the trace is built up; as the leaf primordium elongates and expands, the vascular bundles are extended from the trace outwardly. In the formation of the conducting strands of the leaf, the same types of cells are developed, and the order is approximately the same as in the vascular strands of the stems of the same plant. In leaves, however, there is commonly a larger proportion of the extensible protoxylem elements, especially near the bundle ends. In leaves having secondary growth, this growth takes place soon after other parts of the leaf attain approximately full size.

The Orientation of Vascular Tissue in the Leaf.—In the leaf traces of angiosperms and gymnosperms, as seen in transverse sections of the axis

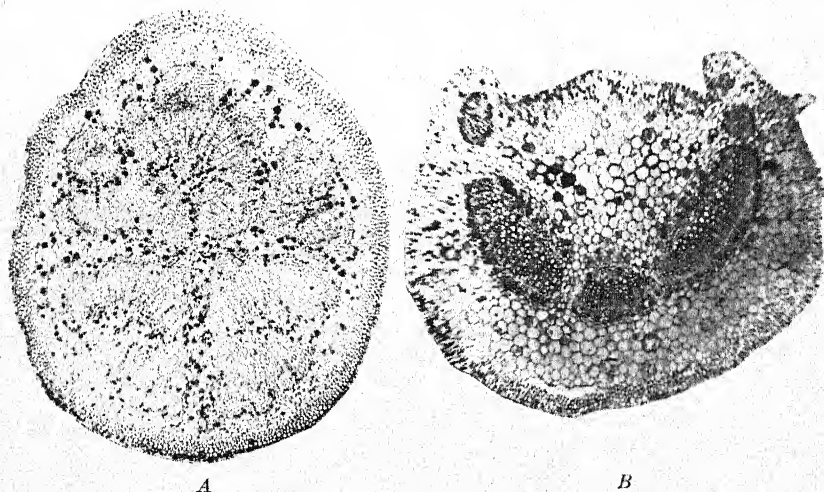


FIG. 122.—Structure of petioles. *A*, *Populus grandidentata*; vascular tissues arranged in cylinders, simulating steles. *B*, *Solanum tuberosum*; vascular tissues in a crescent, normally oriented.

below the level where the traces leave the stele, the phloem is situated toward the outside of the stem. As the traces pass out of the stele and enter the petiole and blade, the xylem and phloem maintain their relative position, so that often in the petiole and usually in the blade the phloem is on the lower side of the leaf and the xylem on the upper side (Fig. 124). Probably because of this orientation of vascular tissues in relation to the stem, the upper side of the leaf is known as the *ventral side* and the lower side is designated as the *dorsal side*. These terms are used in the sense that the ventral side is the side next the axis and the dorsal side that away from the axis.

Although the orientation of the xylem and phloem is fairly constant for typical leaf blades, many variations occur in the petiole, due to the different methods of fusion, division, or twisting of the leaf traces in their course through the petiole. In many instances the traces which enter the petiole separately remain distinct and pass to the blade without change of structure or orientation (Fig. 122, B). In others, however, the traces fuse in the petiole to form a single strand, a hollow cylinder, or a group of more or less complete cylinders (Fig. 122, A); in still others, they divide into several or many strands which become arranged and oriented in any one of many ways. In all these conditions the bundles are frequently amphicribal through the petiole. On passing out of the petiole into the leaf blade the vascular bundles may again assume collateral structure with dorsal phloem; often, however, the petiolar arrangement is maintained through the larger veins.

Stipular Traces.—The vascular supply of stipules is usually derived from the lateral leaf traces, the stipular trace being given off from the leaf trace after the latter has left the stele. Where the stipules are not attached to the petiole, and where they sheath the stem, the stipular trace severs connection with the leaf trace in the cortex. Where the stipule is attached to the petiole and is an integral part of the leaf, the stipular trace may not sever connection with the leaf trace until after the latter has entered the petiole. Except in plants with foliaceous persistent stipules, the stipular traces are usually very much reduced vascular bundles, the xylem consisting of relatively few conducting elements and the phloem chiefly of parenchyma.

Pteridophyte Leaves.—In many ferns, owing to the large size of the leaves, the traces to a single leaf make up a considerable portion of the stele below the point of attachment. These large traces are in most cases a part of an amphiphloic siphonostele, and as soon as they are freed from the stele become amphicribal bundles by the union of the external and internal phloem at the sides of the trace. The external and the internal endodermis also unite about the traces. These bundles pass up the petiole and eventually divide to form the smaller bundles of the compound leaves. Dichotomous branching of the veins is common in the smaller divisions of the leaves of many forms. Ultimately, the minute divisions come into close contact with the mesophyll, much as in angiosperm leaves (Fig. 121, A). In small-leaved pteridophytes, *Lycopodium*, *Equisetum*, etc., the vascular supply consists of a single bundle which passes unbranched to the leaf tip. This bundle is commonly amphicribal.

Sclerenchyma in the Vascular Bundles of Leaves.—Commonly associated with the vascular bundles of petioles and the larger bundles in leaf blades is a varying amount of sclerenchyma. This tissue is apparently very important in strengthening the supporting skeleton of the

leaf blade; the xylem and phloem of the main veins are rarely without it. These mechanical tissues, usually in the form of fibers, occur in strands arranged variously in different leaves and in different parts of the same leaf. One frequent disposition of fibrous tissues in leaf bundles is as a bundle sheath entirely surrounding the vascular strand (Fig. 136, *D*). This condition is common in some types of leaves and in the larger veins of many forms. In this type the sclerenchymatous ring is usually thicker on the dorsal and ventral sides of the bundle than elsewhere, an arrangement which passes, by a series of transitional conditions, into another common type where the fibers occur in two separate strands, one on the dorsal side of the bundle and the other upon the ventral side. In both of these conditions the sclerenchyma often fills the space between the bundles and the epidermis, both below and above. Such an arrangement is considered to be structurally very efficient in strengthening the leaf. Much has been written to emphasize the fact that the arrangement of mechanical elements in leaves and elsewhere is such as to give maximum strength with a minimum amount of mechanical tissue. As the larger bundles divide to form successively smaller and smaller vascular strands, the amount of sclerenchyma becomes very much reduced, until in the smaller bundles mechanical elements are lacking altogether. Some leaves may be further strengthened or stiffened by large branching stone cells in addition, to fibrous strands, scattered through the mesophyll, or by lignified epidermal and subepidermal cells.

Considered morphologically, the supporting elements of leaves and petioles may be formed from any of the tissues. Most commonly, however, the fibrous strands or sheaths which are closely associated with the vascular bundles are either phloem fibers or pericyclic fibers. More rarely, they are derived from xylem or from cortical tissues.

Elements of the Xylem and Phloem in Leaves.—The vascular tissues of leaves are composed for the most part of the types of elements found in homologous tissues elsewhere in the plant body. Thus in xylem the same types of vessels, tracheids, fibers, and parenchyma, both primary and secondary, occur, and in much the same proportion and relation to one another as found in the stele itself. This is true also of the elements of the phloem.

As the bundles branch successively and become smaller and smaller, there is usually a reduction in the relative number of well-developed vessels and sieve tubes as compared with the larger bundles, and also a reduction in the relative amount of secondary tissue as compared with the primary. In the smaller bundles there are no secondary tissues whatever. In fact, secondary tissues may be lacking in all parts of small leaves even though secondary growth occurs elsewhere in the same plant. The primary elements of such small bundles are smaller than are those of the vascular tissues of the stele, and ordinarily a larger proportion of paren-

chyma is present in the leaf. This is especially true of the phloem, which in the smaller bundles may consist wholly of parenchyma.

Bundle Ends.—In the xylem, as the bundles approach their ultimate divisions, the conducting elements become reduced in size and number and consist usually of spiral or reticulate elements only (Fig. 123). These elements become fewer and fewer, and the very tip of the bundle

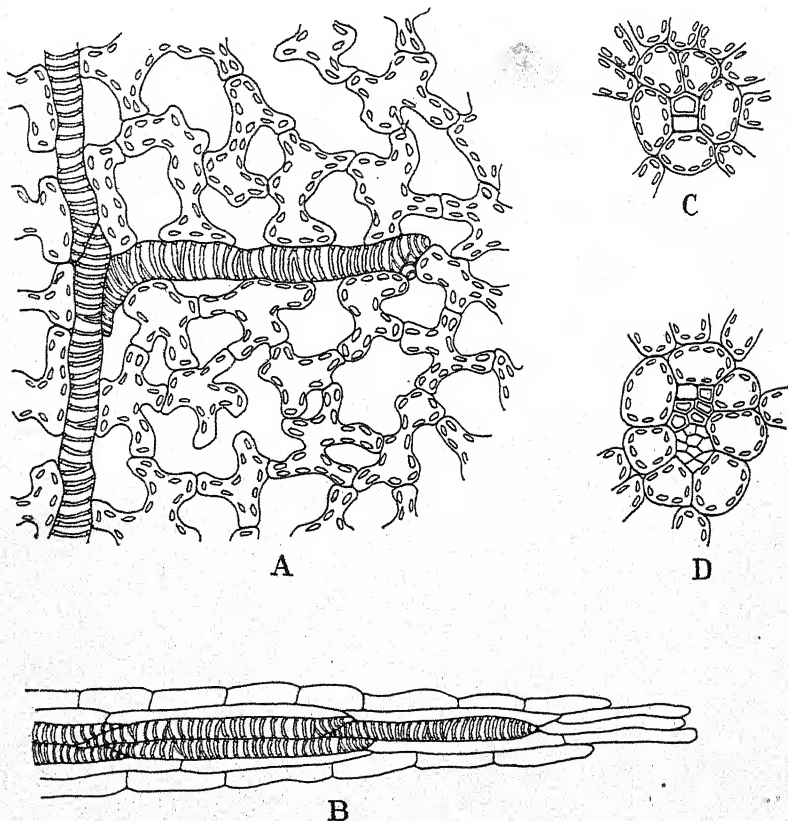


FIG. 123.—Bundle ends. A, B, longitudinal sections in *Oxalis* leaf and *Freesia* petal; tracheids in *Oxalis* unaccompanied by other elements and in direct contact with mesophyll, in *Freesia* surrounded by parenchyma. C, D, cross sections in leaves of *Pyrus Malus*; the bundle sheathed by chlorophyll-bearing parenchyma; C, small bundle made up of one tracheid and one parenchyma cell; D, somewhat larger bundle with phloem.

may thus be composed of a single spiral or reticulate tracheid. A slender bundle tip, consisting of one or few xylem elements, is typically surrounded by parenchyma of a special type, which is supposed to function in the transfusion of water from the tracheid, and also in the collection and conduction of food substances in solution.

In the reduction of the phloem near the bundle end, the sieve tubes become smaller and less definite in form, and the relative size of the

companion cell increases. Finally, a stage is reached where the phloem mother cells, which would ordinarily form sieve tubes and companion cells, do not divide, and a special type of parenchyma cell is formed which resembles the companion cell. To these cells the function of protein synthesis has been ascribed, as well as that of conduction of the photosynthetic products. At the tip of the vascular strand these cells are replaced by the transfusion parenchyma described above. The bundle ends occurring in hydathodes and in glands, especially in the glands of insectivorous plants (Chap. XIV) which function in digestion, have more elaborate conducting and absorbing structures than typical bundle ends.

The vascular skeleton of the leaf with its elaborate branching system with smaller and smaller divisions which ramify to all parts of the photosynthetic tissue shows some similarity to the capillary circulation in animals. The analogy is, however, one of form largely, as in plants there is no closed system comparable to that of the veins and arteries of animals. The vascular system of plants does, however, carry substances, mainly water and mineral nutrients, to the photosynthetic tissue and remove the products of photosynthesis. The exact nature of this circulation, that is, the tissues and cells in which the different substances are conducted, and the method by which conduction takes place is not well understood.

The Mesophyll.—The photosynthetic tissue between the upper and lower epidermis, which consists typically of thin-walled parenchyma, is known as *mesophyll*. This tissue usually forms the larger part of the substance of the leaf. The cells of the mesophyll show great variation in shape and arrangement, but, in general, they are grouped in two classes, the *palisade parenchyma*, or *palisade cells*, and the *spongy parenchyma*, or *spongy mesophyll* (Fig. 124, A, B). In the former the cells are elongate and more or less cylindrical, and arranged in one or more rather regular, compact layers near the ventral, or upper, side of the leaf with the long axis of the cells perpendicular to the leaf surface. In leaves which stand more or less vertically or have a drooping position, palisade parenchyma may occur on both sides. A frequent modification of the columnar palisade cell is the cone-shaped type, which lies with its broad end against the epidermis. In the spongy parenchyma the cells lack regularity in shape and are arranged loosely, so that a large part of their surface is exposed to the gases in the intercellular spaces. Cells of the spongy mesophyll may be very irregular in shape, with radiating arms connecting with the arms of similar cells, thus making an irregular network of green tissue (Fig. 123, A). In many leaves, especially those of plants growing in water or in shaded situations, there is no well-developed palisade parenchyma; this is also the condition in the leaves of most gymnosperms, of grasses (Fig. 124, C, D), and of other specialized types.

The number of palisade layers and the density of the cell structure depends largely, either directly or indirectly, upon light intensity. There may thus be great variation in the proportion and arrangement of the palisade parenchyma in the same species growing under different conditions. There is also often considerable variation in the mesophyll structure of leaves from different parts of the same plant.

Internal leaf structure is, in general, an adaptation to the conditions necessary for photosynthesis. Briefly, these are, in part: first, the

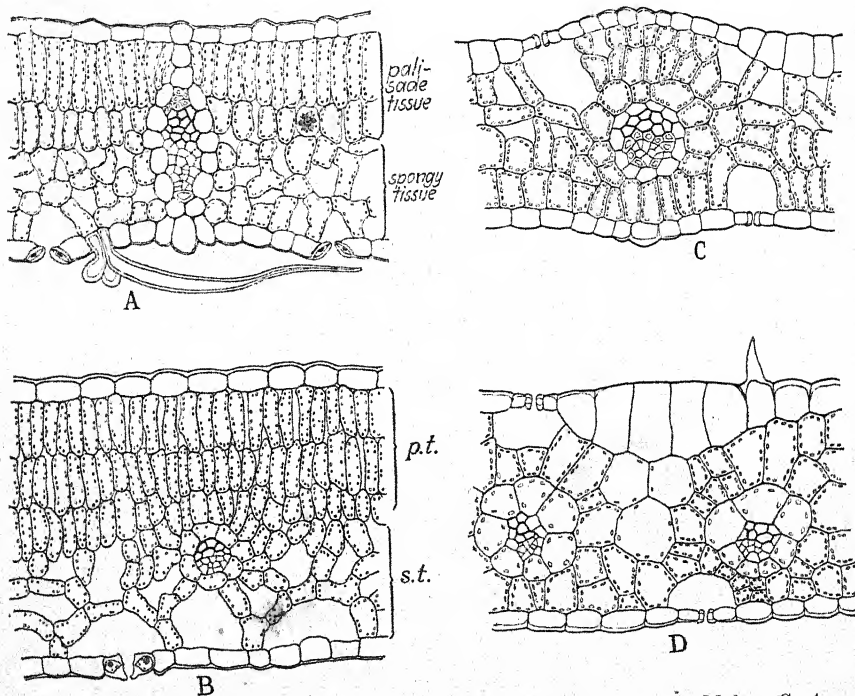


FIG. 124.—Leaf structure, in cross section. A, *Quercus*; B, *Pyrus Malus*; C, *Avena sativa*. D, *Zea Mays*. A, B, with palisade and spongy parenchyma; C, D, without differentiated mesophyll.

exposure of a large number of chloroplasts to sunlight; second, the exposure of a large cell-membrane surface to the intercellular spaces for the interchange of gases; and, third, an arrangement of cells in such a way that the products of photosynthesis may be rapidly removed.

The Arrangement of the Chloroplasts.—In all vascular plants the chloroplasts, the protoplasmic bodies within which the chlorophyll is contained, are fairly uniform in size and shape, being, in the main, minute, and discoid or lenticular. Under conditions favorable for photosynthesis these plastids become arranged about the periphery of the cell with their flat sides against the cell wall which is exposed to the light rays. Under

conditions of excessive light, the position of the plastids may be changed so that the rays fall only upon the edges of the plastid, rather than upon the broad face. Thus where insufficient light is a limiting factor, the maximum surface of the plastids is exposed; and where the light is intense, the plastids may migrate to other positions where they are less exposed. Some plants show extreme variations of mesophyll cell shape, elaborate shape being possibly an adaptation to the exposure of a maximum plastid surface. The irregular cells of the mesophyll of the gymnosperm leaf are familiar examples of this kind of cell (Fig. 138, B, C).

The Relation of Mesophyll Cells to Intercellular Spaces.—The normal structure of the mesophyll is such that a large cell-wall surface is exposed to the "internal atmosphere" of the leaf. The leaf is "honeycombed" with connected air spaces which reach into nearly all parts of the mesophyll. In leaves where the cells of the palisade layers are densely packed, these cells have very little, perhaps no, cell-wall surface exposed directly to air spaces. However, throughout leaves with poorly developed palisade layers and in spongy mesophyll generally, a considerable proportion of the walls of all cells is surrounded by air spaces. In some cases the cells are like short, branching filaments with a minimum of wall surface adjacent to other cells. The air-space system extends, of course, to the stomata. The wall of normal mesophyll cells is of cellulose, or of some similar permeable material, and uniformly thin, so that diffusion may take place through any part. The proportion of wall surface of the mesophyll cells free and exposed in the intercellular spaces varies greatly in different plants, and is, of course, dependent upon the density of the mesophyll itself, which, in turn, varies with the habitat of the plant.

Conduction in the Mesophyll.—The arrangement of photosynthetic cells in close relation to the conducting system is apparently very important from the standpoint of supplying the cells with water and of removing the elaborated food materials. Such is the distribution of the vascular tissue through the mesophyll that all green cells are in fairly close association either with bundle ends or with vascular bundles capable of absorption. In the simplest condition, photosynthetic cells are arranged in such a way that conduction can take place through the cells themselves to a nearby bundle end and thus provide an outlet for diffusible material. The cells of the spongy mesophyll are in many cases particularly adapted for conduction by their branching structure and probably constitute the main channels through which sugars are removed from the palisade layers. Translocated material is conducted through these cells to the parenchymatous sheaths of the bundle ends (Figs. 123, B, C, D; 124); these sheaths, in turn, perhaps conduct the material to the larger vascular bundles. In many plants all of the secondary veins of the leaf which are not entirely surrounded by sclerenchyma have a parenchymatous sheath capable of ready absorption.

More elaborate mechanisms for the removal of synthesized food materials from photosynthetic tissues are frequently found. In one of the common types, specialized parenchyma cells containing little or no chlorophyll are situated so as to connect with a group of palisade cells. Such cells apparently have as their chief function the collection of the products of photosynthesis and the conduction of these to the vascular bundles. Combined with a specialized parenchymatous bundle sheath these cells constitute a rather definite extension of the conducting system within the mesophyll. Certain grasses and sedges have the photosynthetic tissue grouped about the vascular bundles as cylinders or girdles of cells. In such cases diffusion readily takes place directly from the green tissue into the parenchymatous bundle sheath (Fig. 124, C, D).

The Epidermis of Leaves.—The epidermis envelopes the tissues of the leaf with a protective layer broken only by the stomata and the hydathodes. The general nature of this layer, the shape and size of the cells, and the structure and mechanism of stomata have already been discussed in Chapter V. The structure and the occurrence of hairs are also discussed in the earlier chapter. Cutinization and cuticularization have been treated in Chapter II. The epidermis of leaves is, naturally, of the greatest importance because of the nature of the soft mesophyll tissues within, which perish through desiccation almost immediately upon injury to the protective layers. The modifications of the epidermis which occur as adaptations to different environments, especially in xerophytes, are discussed in Chapter XIV under Ecological Anatomy.

The Distribution of Stomata on Leaves.—In dicotyledonous leaves of the broadly expanded type, stomata normally occur in largest numbers upon the lower or dorsal side. Some species have comparatively few on the upper or ventral side and some lack stomata on the upper surface altogether. Plants with leaves which stand in a nearly vertical position may have stomata about equally distributed on both surfaces. Many of the monocotyledons have leaves of this type. Floating leaves of aquatic plants have stomata upon the upper exposed surface only, and submerged leaves lack stomata. In general, the distribution of the stomata depends upon the environment to which the plant is adapted, those adapted to living under more severe conditions as regards drying out having stomata in the more protected positions on the plant.

✓ In the majority of leaves, stomata are arranged apparently without regularity. In some plants, however, as, for example, the grasses, stomata may be situated in regular rows, each stoma oriented in the same way. Xerophytes and some other plants often have stomata in groups or furrows which are protected in various ways. The number of stomata per unit area of epidermis varies greatly. Some plants, mostly xerophytes, may have as few as ten to fifteen per square millimeter. At the other extreme, species of *Spiraea* have been reported with as high as

1300 stomata per square millimeter. Between these extremes all conditions exist, the common number being about 250 per square millimeter as found in the apple and plum under ordinary mesophytic conditions. Apparently, the number of stomata per unit area bears no definite relation to habitat, other factors being of greater importance in determining the number.

The Grass Leaf.—Among the many types of leaf structure which vary from that commonly found in dicotyledons, that which occurs in the grasses and sedges and that of the gymnosperms are of sufficient importance to warrant special treatment. Gymnosperm leaves of practically all species are, however, xerophytic in their structure, and hence are discussed in Chapter XIV.* The leaves of the grasses are alike in general structure, variations being the result of adaptation in various ways to xerophytic or other ecological conditions. Fundamentally, the grass-leaf blade consists of a skeleton of parallel vascular bundles between which spongy mesophyll is supported (Fig. 124, C, D). The bundles are of nearly the same size throughout their length, and, except for occasional small anastomosing strands, are separate from one another. Frequently, the leaf blade has a large median bundle associated with a pronounced midrib projecting on the dorsal side. The other bundles may be of two or three types, but differ chiefly only in the amount of mechanical and conducting tissue present. The smaller bundles are spaced alternately between the larger. The entire leaf consists of a sheathing base and a linear blade; the former surrounds the culm for some distance and merges in a more or less prominent joint with the leaf blade, which is set at an angle with the culm.

Sclerenchyma in the Grass Leaf.—The sclerenchymatous tissues of grass leaves are ordinarily arranged in conjunction with the vascular bundle as two strands of tissue, one on the dorsal and the other on the ventral side. In the case of the larger bundles, and frequently in the case of the smaller also, the fibrous strands extend from the epidermis to the bundle on both sides, so that together with the bundle they form a bar of hard tissue extending through the leaf from ventral to dorsal side, a structural condition considered to be mechanically very efficient. In the smaller bundles the amounts of sclerenchyma and conducting tissues are proportionately reduced. Only rarely do the bundles lack sclerenchyma altogether.

Bundle Sheaths in the Grass Leaf.—Among the characteristic features of grass leaves are the tissues immediately surrounding the vascular bundles. These occur commonly as two layers of cells, each one cell thick, completely surrounding the bundle next the vascular tissues (Fig. 124, C). The inner sheath is more or less thick-walled and lignified, resembling an endodermis in its general appearance. Whether this is an endodermis in the strict morphological sense is questionable. The

thickening on the walls of the cells of this layer is frequently heavier upon the inner and radial walls than upon the outer, although in some cases it extends entirely around the cells. Various functions have been ascribed to this layer, but protection against crushing, especially of the softer phloem cells, is the most probable. In bundles with well-developed sclerenchyma this lignified sheath abuts directly upon the fibrous strands, thus adding rigidity to the whole structure by completing the so-called "girder structure."

The outer sheath, often known as the *mestome sheath*, is made up of thin-walled parenchyma cells, which appear mostly isodiametric when seen in transverse sections of the leaf, but much elongated as seen in longitudinal section. These cells form about the bundle a parenchymatous girdle, to which is ascribed the function of conducting the soluble food products from the specialized photosynthetic tissues to the conducting tissues. In well-developed bundles of some species the cells of this girdle lack chlorophyll, and are hence readily recognized. In the smaller bundles the cells may contain chlorophyll, but usually in less amount than other photosynthetic cells.

The Mesophyll of the Grass Leaf.—In the leaves of grasses, as in other leaves, the photosynthetic tissue fills the space between the vascular bundles more or less solidly. Ordinarily in grass leaves there is no well-developed palisade layer of elongate cells such as is characteristic of dicotyledonous leaves generally. Frequently, however, there is a weakly developed palisade layer next the epidermis on one or both sides of the leaf. The cells of these layers are nearly isodiametric and differ from the spongy mesophyll cells chiefly in that they are compactly arranged, whereas in the spongy mesophyll there are many intercellular spaces. The cells in the latter tissue are also frequently irregular in shape, forming branching systems for conduction, as in analogous tissues of other types of leaves. In some species of *Cyperus* and in a few xerophytic grasses the green tissues themselves are arranged in a sheathing girdle about the vascular bundle.

The Epidermis of the Grass Leaf.—Although variations in the structure of the epidermis of the grasses occur rather frequently, especially in plants adapted to growth in extremes of environmental conditions, the general features are fairly constant. The epidermal cells are for the most part elongate-rectangular in shape, being nearly square as seen in transverse section, but in longitudinal section much elongated. They are arranged in regular rows extending lengthwise of the leaf. Over the vascular bundles the cells are often smaller and thick-walled, to some extent resembling sclerenchyma. Great variation occurs in the extent of cutinization. In surface view of the leaves the cells do not show marked irregularity of outline such as is shown in the epidermis of many dicotyledons.

A type of cell common to many species is the so-called *motor cell*, or *bulliform cell*, which, apparently, constitutes the mechanism which functions in the rolling of grass leaves in dry weather (Fig. 124, C, D). These cells have much more depth than the ordinary epidermal cells and are arranged in rows extending throughout the length of the leaf upon its upper surface, frequently lying at the bottom of well-defined grooves. The cells are thin-walled and lack chlorophyll, and by the decrease in their turgor permit the upward and inward rolling of the leaf. Some species possess only one or two rows of this type of cells, whereas others have many. Few species lack them altogether. At the edges of the groups of motor cells as seen in cross section of the leaf, there are cell types transitional between typical motor cells and the ordinary epidermal cells.

Arrangement of the Stomata in the Grass Leaf.—The type of stoma found in the leaves of the grasses is surprisingly uniform, considering the diversity of habitat in which grasses are found. The structure of the stoma of the grass type is given in Chapter V (Fig. 54, I, J, K). The stomata in the leaf are usually arranged in rows extending parallel to the long axis and interspersed between the elongate epidermal cells. Frequently, several rows of stomata are spaced close together between wider bands of epidermal cells. Although in a considerable number of cases stomata occur upon both surfaces of the leaf in approximately equal numbers, in the majority of species these openings are more numerous in the upper epidermis and in some species, chiefly xerophytic, may be wanting upon the lower side.

Hairs of various types are common in the epidermis of many species. Short, stiff projections which give the surface of the leaf a harsh texture are particularly common. In some forms these teeth give the leaf margin an effective cutting edge, as, for example, in species of *Leersia*.

The Persistence of Leaves.—A large proportion of the gymnosperms, a few broad-leaved, temperate-zone plants, and many tropical forms, generally hold their leaves for more than one season. In evergreen plants possessing secondary growth, as is the case with the gymnosperms and dicotyledons, the persistence of leaves for any length of time involves the lengthening of the leaf trace as successive annual layers of xylem are added by the cambium. This lengthening is accomplished by the activity of a special meristematic layer in the trace itself (Chap. VI). Ordinarily, the needle leaves of the gymnosperms and the broad leaves of angiosperms do not persist more than three to five years, after which time they are cut off by abscission layers in the same manner as are deciduous leaves. In a few cases evergreen leaves may persist for many years, as, for example, on the trunks of *Araucaria*. In the ferns and some of the palms and other monocotyledons the leaves may persist for a considerable number of years, the older leaves gradually ceasing to function.

Many of these are not cut off by abscission layers but cling to the stem until they disintegrate by weathering. The leaves of many annual and perennial herbs are also "withering persistent." In the majority of temperate-zone plants, both woody and herbaceous, the leaves function for but a single season. A discussion of leaf abscission is to be found in Chapter IX.

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CHAPTER XIII

THE FLOWER—THE FRUIT—THE SEED

THE FLOWER

The flower is, morphologically, a determinate branch with crowded appendages, the internodes being much shortened, or in many cases obliterated. The appendages are modified in function and appearance, and the upper ones are often so placed as to appear terminal on the axis. Anatomically, however, the flower is a typical stem with appendages; in no fundamental way does it depart structurally from the normal stem with leaves.

The Vascular Skeleton of the Flower.—In structure, the pedicel is a typical stem, herbaceous or woody, with a ring of vascular bundles or with an unbroken cylinder of vascular tissue. In the receptacle the stele is modified in shape, often expanding and becoming like an inverted or flattened cone or pyramid. From this receptacular stele depart the traces to the various floral organs (Fig. 125, A, C), traces which in origin, structure, and behavior are similar to those of leaves. Gaps accompany the exit of these traces, and the crowding of the organs thus breaks the cylinder up into a network of strands (Fig. 125, B). The traces pass off successively to sepals, petals, stamens, and carpels, according to the manner of arrangement of these parts in the flower, that is, in whorls or in spirals, as the case may be. However, many parts which to external inspection are apparently whorled, such as the petals of some Ranunculaceae and the stamens of the Rosaceae, may be seen from anatomical evidence to be arranged in flat spirals. The method of origin of the traces to the different flowers is essentially alike in all cases. The number of traces, however, to the various types of organs is markedly different, and is also different from that to the normal lateral appendages, the leaves, of the same plant. Thus, typically, petals and stamens possess a single trace, carpels three traces, and sepals usually the number of traces possessed by the leaves of the plant in question (Fig. 125, B). In all these organs the constancy of number of traces throughout the angiosperms is remarkable, and is indicative of morphological unity and conservatism. Thus, there is a single trace in the stamen and petal without regard to size, shape, nature, or persistence of these organs. Exceptions occur for the stamens in some of the Magnoliaceae, where there are three traces, and for the petals in a considerable number of families. For the petal, the exceptions are chiefly those in which the

petals are sepal-like, and are without doubt sépaline in nature. The three traces of the carpel are found so modified in many plants that there is but a single trace. This condition is found where the carpel is reduced in size and in number of ovules, as in achenes. In these cases it is apparent from comparative studies that in such carpels the vascular supply, like the rest of the carpel, has been reduced, two of the traces having disappeared in the evolutionary modification. Of the normal three

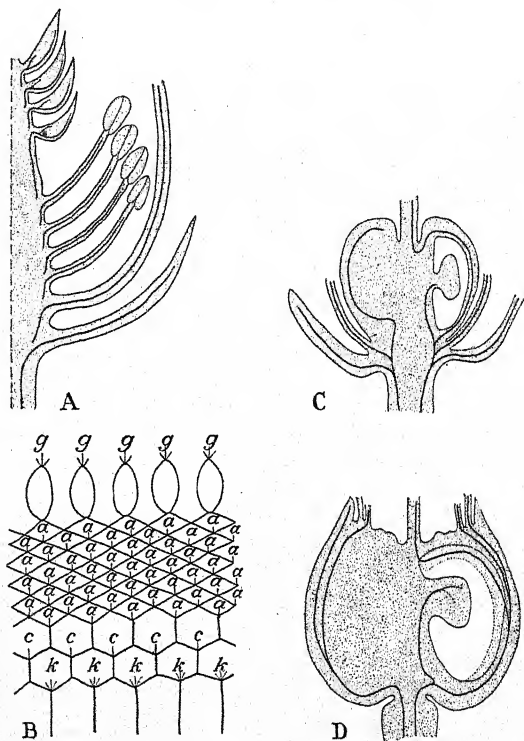


FIG. 125.—Vascular system of flowers. A, half of median longitudinal section of flower of *Ranunculus*. B, vascular system of axis of flower of *Aquilegia canadensis*, split open and spread out in one plane; the traces to the floral organs are shown: *k*, to sepals; *c*, to petals; *a*, to stamens; *g*, to carpels. C, vertical section of base of flower of *Pyrola secunda*, showing origin and course of traces to floral organs in a hypogynous flower. D, the same in *Vaccinium pennsylvanicum*, showing course of bundles in an epigynous flower. (A and B after Smith; C and D after Hancy.)

traces to the carpel, the median is called the *dorsal trace*, since the carpel is a leaf folded toward the ventral surface. The two lateral traces are called *ventral* or *marginal traces*, since they run along the ventral side of the folded carpel and on or near the margin of the leaf. These traces depart from the stele of the receptacle higher up than does the dorsal trace.

Because of the large number of traces departing close together to the crowded floral organs, the vascular skeleton of most flowers is very

complex. But in many cases it is rendered more simple superficially, though actually still more complex, by the fusion of adjacent traces in their proximal parts. In the study of flower morphology, two types of fusion of floral organs are recognized—cohesion, where members of the same whorl are fused to one another; and adnation, where members of a whorl are fused to members of a different whorl, above or below. This condition of fusion of appendages to other appendages is looked upon as a condition of specialization in the evolutionary development of the flower. Varying types and amounts of such specialization occur in the more advanced families. In cases of such external fusion it is found that the

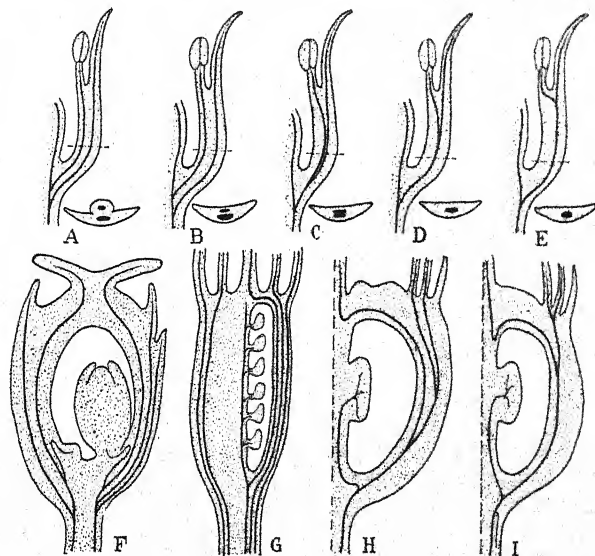


FIG. 126.—Diagrams to show fusion of bundles under adnation. A to E, series showing fusion of stamen and petal and of their bundles. F to I, ovaries of epigynous flowers: F, vertical section of flower of *Juglans*, showing no fusion of bundles of floral organs; G, of *Alstroemeria*, similar; H, I, of *Vaccinium vacillans* and *V. macrocarpon*, showing fusion in their proximal parts of the bundles of floral organs. (G, after Van Tieghem; H, I, after Hancey.)

internal parts, even the vascular bundles, are often likewise fused. Thus, in epipetalous stamens the basal part of the petal will, in some cases, show two traces, one the stamen trace, superposed to the other, the petal trace (Fig. 126, A, B, C). In such a case there may be definite structural evidence, in a histological separation, that the base of the petal really represents the fused bases of petal and stamen, or there may be no evidence other than the presence of the two bundles. In another similar petal bearing a stamen there will be found but a single vascular bundle in the base of the petal. Neither the bundle itself nor any of the surrounding tissues may show evidence of the morphologically double nature of the bundle (Fig. 126, D, E). This fusion of bundles may

extend only a slight distance from the base of the petal, or as far as the free base of the stamen, even to the anther when this is sessile. Fusion appears to take place first externally, ultimately becoming more intimate and involving also the vascular skeleton. In cohesion, similar fusion of bundles often takes place, and apparently more readily so than in adnation. For example, the folding of the carpel brings close together the two marginal carpellary bundles (Fig. 127, *A, C*); these commonly fuse (Fig. 127, *B, D*), so that the carpel, though possessing three traces in the receptacle, has but two vascular bundles running through its free part (Fig. 127, *E*). The ventral bundle, formed thus of two, may give evidence of its double nature in its structure, but often appears as a simple, large bundle, perhaps even larger than the dorsal bundle, since

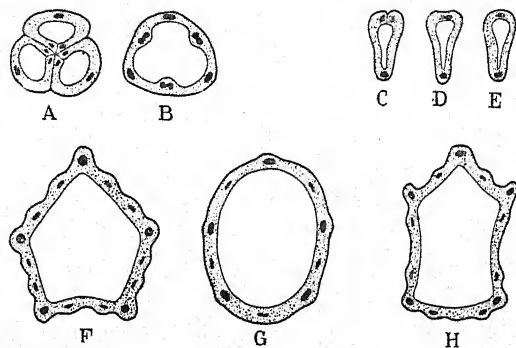


FIG. 127.—Diagrams showing fusion of adjacent bundles in cohesion. *A*, three-celled ovary, each carpel with its dorsal and two ventral bundles, all free. *B*, three-carpellate ovary, the ventral bundles of adjacent carpels fused in pairs, the fusion incomplete. *C, D, E*, carpels showing approximation and fusion of ventral bundles. *F, G, H*, cross-sections of calyces of mint flowers: *F*, of *Monarda didyma*, showing fifteen bundles, the adjacent marginal bundles of the sepals all remaining free; *G*, of *Physostegia virginiana*, showing all laterals fused in pairs, only ten bundles being present; *H*, of *Salvia patens*, the marginals of the uppermost sepal fused with those of adjacent sepals, the others free, thirteen bundles being present.

it supplies the placenta. | Similarly, when carpels are fused edge to edge as open structures to form a one-celled ovary, the lateral bundles of adjacent carpels may fuse, and the three-carpelled ovary, though supplied with nine traces, has but six bundles (Fig. 127, *B*), and not nine, as would be the case if no fusion occurred. Again, in the gamosepalous calyx of the Labiatae, the lateral traces of the sepals fuse in pairs to a greater or less extent; thus there are found in the mint family varying numbers of "ribs" on the calyx tube, ten if every pair fuses, fifteen if none fuse, and numbers between these if part of them fuse (Fig. 127, *F, G, H*). It is partly on this anatomical basis that genera in this family are separated taxonomically.

It is thus apparent that, when bundles lie close together and the organs they supply have become fused, these bundles tend also to fuse.

Such union clearly follows—though slowly—the external fusion. The vascular structure of simple flowers, then, in which cohesion and adnation have occurred, must be interpreted on the basis of possible internal fusion similar to the external. This is to be looked for in the fusion of bundles lying side by side at the same level, that is, in the same whorl, as in the cases cited, and in those lying above and below one another in the same radius, as in the case of petal and “opposite” stamen. Thus lateral bundles of carpels, sepals, and of petals (when petals possess three or more traces) may be found fused with the lateral bundles of adjacent members of the same whorl; likewise, the median bundle of the carpel,

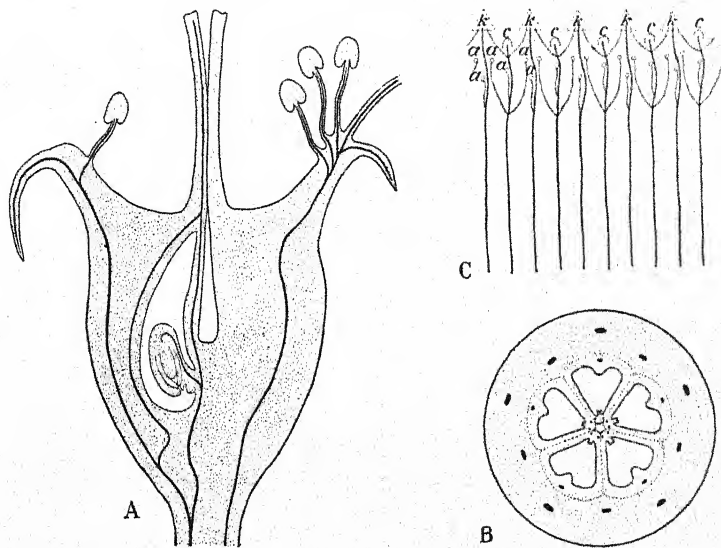


FIG. 128.—The vascular system of the flower of *Pyrus Malus*. A, vertical section. B, median cross section. C, vascular system, exclusive of carpellary supply, spread out in one plane—*k*, *c*, *a*, bundles to sepals, petals, and stamens respectively. (C, after Kraus and Ralston.)

the bundle of the stamen of the second row below, and the median bundle of the sepal may fuse; also the bundle of the petal and of its opposite stamen may fuse, together sometimes with the lateral bundles of the sepal and of the carpel which lie in approximately the same radius. Thus there may be found extensive fusion of the traces to the floral parts (Figs. 125, D; 126, H, I). This condition is most extreme in the case of flowers with inferior ovaries where adnation of all the whorls has occurred, as in the apple (Fig. 128). It is on a basis of interpretation along these lines—which cannot be gone into in detail in this treatise, since they deal wholly with comparative morphology—that evidence is derived to show that the inferior ovary, in many cases at least, is not of receptacular nature. In these forms the wall of the inferior ovary con-

sists morphologically of the basal portions of all parts of the flower. The ovary may clearly show structurally that it is made up of all these parts, at least the vascular skeleton of each being present, as in the Juglandaceae (*Juglans*—Fig. 126, *F*) and Araliaceae (*Hedera*), or it may be very simple in structure histologically and anatomically, in the latter respect closely resembling a stem in its bundle structure. In this latter case each bundle represents a set of traces which supply a radial group of organs fused phylogenetically.

The Petal and the Sepal.—The petal is, in general appearance and external structure, a leaf, and, though considerably modified, is histologically closely similar to that appendage. The vascular system is often reduced in amount and in supporting cells, the bundles being otherwise similar to those of leaves. This reduction accompanies that of the mesophyll which commonly consists of but a few rows of cells. The cells of the mesophyll are very loosely arranged and rarely show a

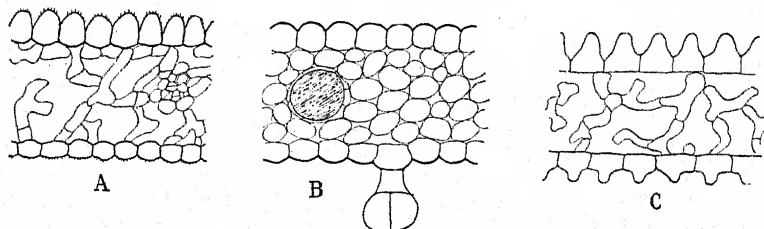


FIG. 129.—Cross sections of petals. A, *Amelanchier laevis*. B, *Lysimachia Nummularia*, showing glandular hair and secretory chamber. C, *Pinguicula vulgaris*.

palisade layer (Fig. 129). Delicate petals may have but one to three indefinite layers of mesophyll. Thick and fleshy petals may closely resemble fleshy leaves in structure, and may even contain sclerenchymatous cells. Except in petals that are green or greenish in color, no chloroplasts occur in the mesophyll. Secretory cells and tissues are, of course, frequent in all floral parts. The epidermis of petals resembles that of normal leaves, though in form of cells there is a greater range. Cells with undulate, toothed, and stellate or irregularly lobed outline are common, especially in the more delicate flowers (Fig. 130). This structural condition perhaps results in a stiffening of the organ where mechanical support of other types is lacking. Stomata occur on most corollas, often on both the upper and the lower surface, though in very thin petals they may be vestigial. The guard cells of petaline stomata do not possess chlorophyll, however, except when the mesophyll also contains chloroplasts. A cuticle is present in nearly all cases, though this varies greatly in thickness in different plants. The epidermis of petals frequently shows intercellular spaces of various size, shape, and abundance. These lie commonly in the "loops" and lobes of the irregular cell

wall (Fig. 130, C, D, E, F). Such spaces do not open to the outer air, however, since they are covered in all cases by the cuticle. Hairs of all types occur freely upon petals, the papillose type being very common. These very short hairs (Fig. 129, C) are responsible for the "velvety" appearance of petals. The sepal resembles the petal in structure, but is generally more leaf-like.

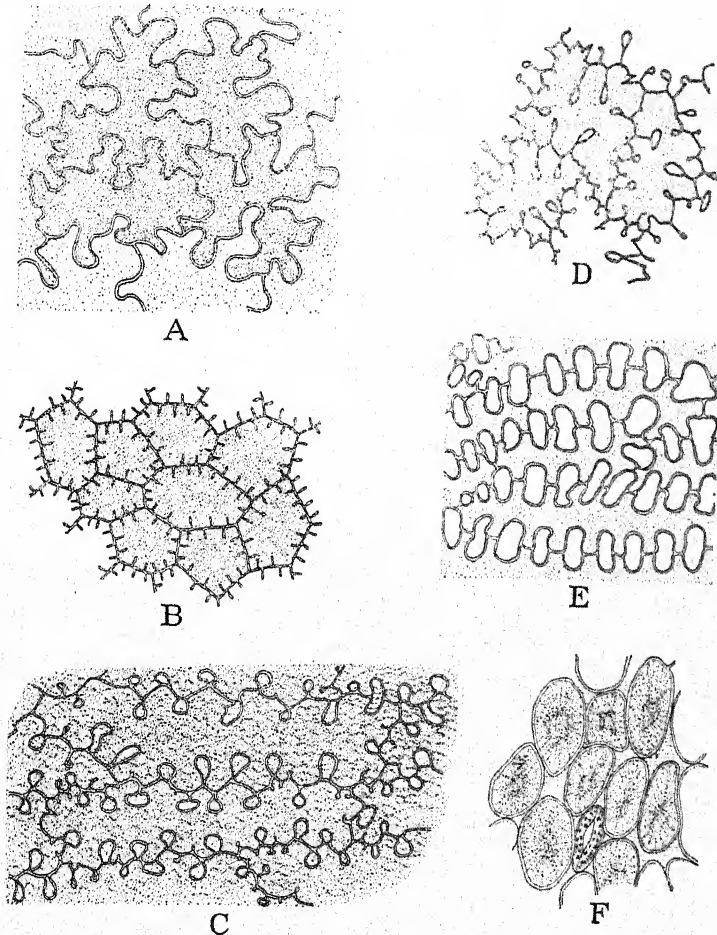


FIG. 130.—Epidermis of corolla. A, from *Calceolaria*. B, from *Pelargonium*. C, from *Clarkia*. D, from *Anchusa*. E, from *Linum*. F, from *Erythrina*. (After Hiller.)

The Stamen and the Pistil.—The single traces of the stamens commonly pass as unbranched bundles to the anther; however, in more or less fleshy stamens, such as those of *Magnolia*, small lateral branches extend into the surrounding unspecialized parenchyma. The traces of the carpels may pass unbranched through the ovary and style, but

frequently branch more or less freely, many carpels having a vascular skeleton much like that of leaves. The epidermis of stamen and pistil is of typical structure, the cells usually with straight walls and with thin cuticle or without such covering. Stomata occur on stamens only when these structures are expanded and leaf-like. In pistils, however, they occur freely on the outer surface and are even found in the epidermis lining the ovarian cavity. The bundles supplying the stamen and pistil, like all small bundles of the flower, tend to be amphicribal. In the stamen, the bundle extends to the anther; in the pistil, one or more of the bundles usually pass through the style and enter the stigma. Vestigial strands are sometimes found. These are the weak or abortive bundles representing the supply to organs, such as additional sporophylls and ovules, lost in the course of evolutionary modification.

THE FRUIT

A fruit is a developed and ripened ovary or ovaries, with the addition, in many cases, of adjacent floral parts likewise modified in nature. The structure of a fruit is, therefore, fundamentally, that of the floral parts from which it has developed. For example, a fruit developed from a single carpel has the general structure of a single carpel; it is, in fact, merely an enlarged carpel with its parts increased in size, though in varying proportion. In nearly all cases the morphological nature of a fruit may readily be determined from the mature fruit alone if anatomical characters be considered. At least, the outlines of carpels, receptacle, sepals, etc., are visible, and the vascular supply remains essentially the same. The development of the fruit has involved the enlargement and often the distortion of the various parts of the carpels and of the stem to which these modified leaves are attached. The fruit thus consists fundamentally of swollen and distorted leaves, and, though this structure is normally more or less clearly evident, the terms used in description of leaf structure are not applicable and are supplanted by special terms. Thus the body of the fruit developed from the ovary wall, which surrounds and encloses the seed, is known as the *pericarp*. When this is not homogeneous histologically, and distinct outer, inner, and median regions are evident, these regions are known as *exocarp*, *endocarp*, and *mesocarp*, respectively. The terms "exocarp" and "endocarp" are sometimes applied to the outer and inner epidermis respectively when these differ from adjacent tissues, but are most often applied to regions of several layers of cells, whether or not the epidermis be included. Each of these parts may consist of parenchyma or sclerenchyma, or of complex tissue of various types. In many cases the pericarp is not separable into parts, being more or less homogeneous; in other cases only exocarp and endocarp are evident. In a berry the entire pericarp is parenchymatous; in

a drupe, there is a parenchymatous exocarp and a sclerenchymatous endocarp. In neither of these types is a mesocarp differentiated. In fruits an outer epidermis is always distinct, as is an inner epidermis which lines the ovary cavity. These layers may or may not partake of the nature of the adjacent pericarp tissue. Each of these, especially the outer, is often reinforced by a hypodermal layer.

The Vascular Skeleton of Fruits.—A fruit possesses the vascular supply of the floral parts from which it has been derived. This vascular supply is strengthened and extended as the fruit develops, the diameter of the bundles being increased either by primary or secondary growth, or by both these methods of increase, and the bundles extended by terminal primary growth and by the addition of branches through the newly formed tissue. The main vascular system of a fruit, however, though often obscured by branches, remains fundamentally the same as in the flower. Thus, where there are fifteen simple bundles in an ovary of five carpels, there are fifteen large bundles with numerous anastomosing branches in the fruit developed from that ovary. The smaller branches extend throughout the pericarp as the smaller bundles of a leaf spread throughout the mesophyll. The ultimate branches, like those in a leaf, are very slender and consist of but few elements, these being chiefly protoxylem cells accompanied by a very few elongate parenchyma cells. Where the pericarp is fleshy, these finer bundles appear to be more numerous than in dry fruits.

The Epidermis of Fruits.—Both the inner and the outer epidermal layers of fruits closely resemble the epidermis of stems and leaves in form and content of cells, in wall structure and cuticle, and in the presence of stomata. The inner epidermis is more delicate than the outer, but often has a thin cuticle and stomata. In dry fruits the inner epidermis may be thick-walled, whereas in fleshy fruits it may in the last stages of ripening break up into individual cells. The cells of the epidermis are most commonly isodiametric, polygonal cells, as in the Rosaceae, Compositae, Liliaceae, and Rubiaceae. In the Ranunculaceae, some Scrophulariaceae, etc., the cells are sinuous in outline, lobed and dovetailed with one another, as in the epidermis of some petals and leaves. In berries and drupes, and probably in other fleshy fruits, the epidermal cells are polygonal and very small with rather thin walls, for example, in *Rubus*, *Vitis*, *Ribes*, *Vaccinium*, and *Cornus*.

Periderm in Fruits.—In a few fruits of the "russet" type a periderm layer arises in or close below the epidermis and is apparent on the ripe fruit as a rough, brownish layer, as in russet apples and pears, in *Achras* and *Calocarpum*, the sapotes, and in other tropical fruits. In the form of lenticels restricted periderm occurs in apples and pears where it forms the "dots" on the fruit. Corky ridges, nodules, etc., which represent developments of phellem, occur on many dry fruits, as in *Circaea* (Fig. 131).

The Pericarp.—Regardless of the morphological nature of the fruit, in histological structure the ripe pericarp may be either parenchymatous and succulent, or sclerenchymatous and parenchymatous, but not succulent. On this basis fruits are called *fleshy* and *dry* respectively. Further classification is made on the basis of morphological nature, method of dehiscence, etc. Only classification on a basis of structure is concerned in the present discussion.

Dry Pericarp.—The three characteristic layers of the pericarp are more commonly present in dry fruits, where sclerenchyma and “dry” parenchyma are abundant, than in fleshy fruits. These three layers vary in nature and in extent in different fruits, being either sclerenchymatous or parenchymatous, and ranging from one layer to many layers in thick-

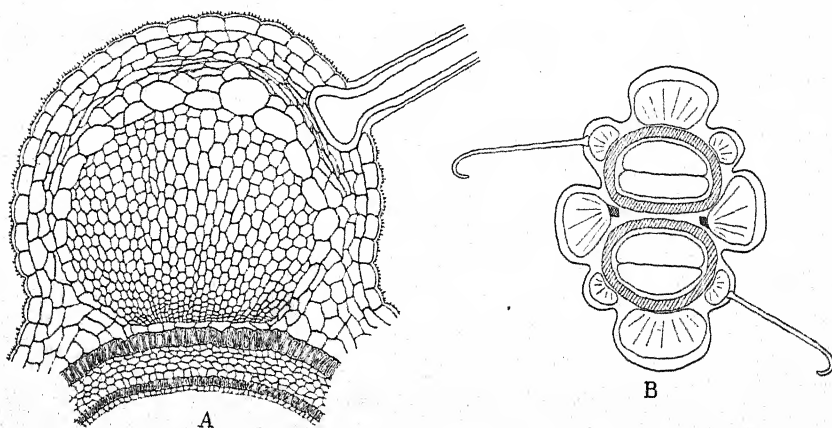


FIG. 131.—Dry fruit of *Circaea latifolia*. A, detail of portion of the cross section (B) of entire fruit, showing the pericarp with its various layers, the ridge of corky secondary tissue, and the large, rigid hairs.

ness (Fig. 131). The parenchyma cells may be closely appressed to one another, or loosely arranged with prominent intercellular spaces. The sclerenchyma cells are of all types of fibers and stone cells, and may be mingled in any way. Often there are found, especially in exocarp, successive layers of different types of sclerenchyma—sometimes including layers of parenchyma—in each of which the cell shape and type, or the direction of the long axis of the cell is different. The resulting structure is apparently very strong from the standpoint of mechanical protection. In many fruits the mesocarp consists of two parts, so that the pericarp is essentially four-layered, as is the case in the achenes of the Compositae. In winged fruits that portion of the pericarp constituting the wing is usually of firm but light structure. In these fruits the supporting cells are chiefly those of vascular bundles with their fibrous sheaths. Between these bundles loose tissue, with intercellular spaces, is frequently present. In many dry fruits the thin-walled parenchyma col-

lapses to a greater or less extent as the fruit dries in maturing. When the fruit is a firm, thin capsule, as in the Caryophyllaceae, Juncaceae, and Cistaceae, the epidermal layers and the pericarp are made up largely of close-packed, thick-walled cells. No stomata occur in such cases.

Fleshy Pericarp.—In fleshy fruits the entire pericarp becomes soft and juicy, or some parts ripen in this way, the other layers becoming dry or stony. The fleshy layer may be homogeneous, as in the apple and peach, or the pericarp may consist of mingled succulent parenchyma and stone cells in varying proportions, as in the pear, quince, huckleberry

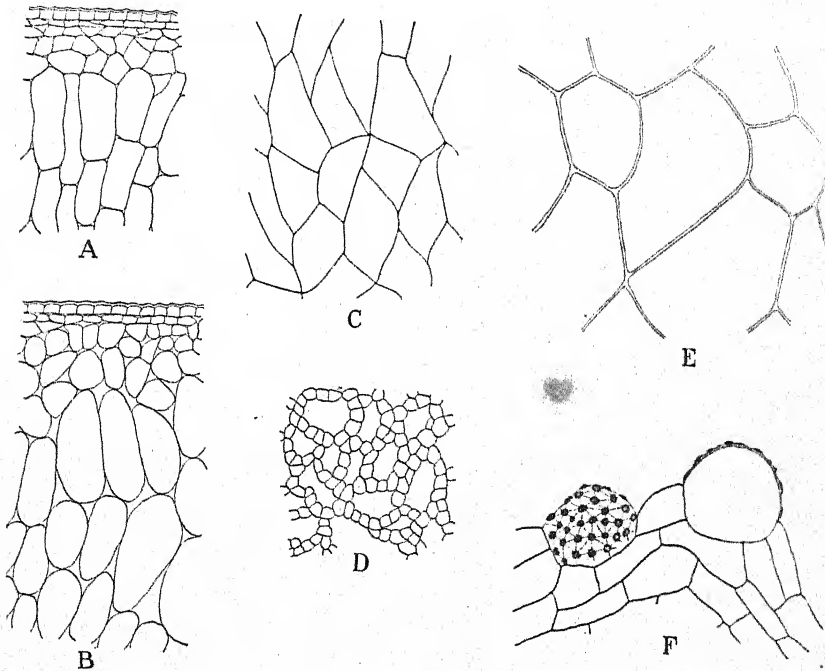


FIG. 132.—Fleshy pericarp. A, B, ripening and ripe outer pericarp of *Prunus Cerasus* (var. Montmorency). C, ripe, fleshy pericarp of *P. Cerasus* (var. Morello). D, "dry," fleshy pericarp of *Zizyphus* (jujube). E, fleshy pericarp of *Citrullus*. F, outer pericarp and epidermis of fruit of *Floerkia*; the walls of some epidermal cells with prominent centripetal thickenings.

(*Gaylussacia*), and black walnut. The fleshy cells are in all cases parenchyma cells, usually with very thin walls, more or less turgid with fluids. When the fruit is ripe, these cells frequently are more or less separated from one another (Figs. 132, B; 133, C, F), so that the tissue is soft and loose; large and definite air chambers, as in *Zizyphus* (Fig. 132, D), are, however, uncommon. In many fruits, even in very soft types, such as persimmon, grape, and some varieties of sour cherry, there is no separation of cells at maturity (Fig. 132, C). In other fruits, like the watermelon (Fig. 132, E), the cells are very large and firm-walled, and when

very ripe separate in certain regions. Many non-succulent fleshy fruits, such as the checkerberry (*Gaultheria*), species of *Crataegus*, etc., have abundant intercellular spaces, and the cells of the flesh are not turgid, having perhaps shrunk in ripening.

Whether or not the fleshy pericarp is homogeneous, there are commonly in fleshy fruits three, four, or five distinct layers. In berries only the outer and inner epidermis and the fleshy layer may be distinct, as in fruits of the Solanaceae, (tomato, red pepper, ground cherry, etc.). More often a hypodermis of one to four rows of cells lies under the outer epidermis (Figs. 132, *B*; 133, *C*). This layer consists usually of parenchyma cells, differing in size and shape from those below, and sometimes with walls so thickened as to have a collenchymatous appear-

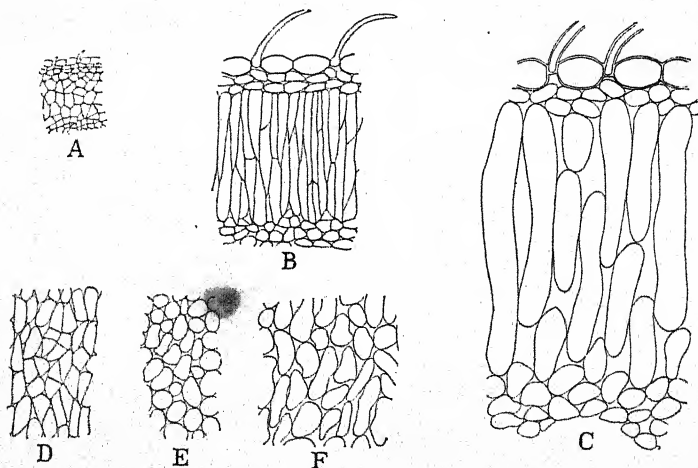


FIG. 133.—Fleshy pericarp. *A, B, C*, successive stages in the development of the exocarp of *Rubus strigosus*; *A*, green fruit soon after fertilization; *B*, half-ripe fruit; *C*, ripe fruit, all sections radial and drawn to same scale. *D, E, F*, fleshy receptacle of *Fragaria*: *D*, half-ripe fruit, radial section; *E, F*, ripe fruit, tangential and radial sections, respectively.

ance. In a few fruits, as in the pear and the Japanese persimmon, a hypodermis containing sclerenchyma is present. A parenchymatous hypodermis usually merges into the underlying parenchyma. In stone fruits the hard endocarp makes an additional layer. Further, this layer is often made up of two or more distinct layers in which different cell types occur, such as stone cells and fibers, or similar cells differently oriented, for example fiber-like stone cells with the long axis horizontal in one layer and vertical in another.

The Epidermis of Fleshy Fruits.—The outer epidermis of fleshy fruits is made up of small, rather thick-walled, mostly isodiametric cells. These contain abundant tannin when immature, but commonly lose this when mature. The number of stomata in the epidermis of fruits varies much—from many, as in *Pyrus*, to none, as in *Vitis*, *Lonicera*,

Vaccinium, and *Gaylussacia*. In berries the inner epidermis though difficult to recognize, generally persists in the ripe fruit. In drupaceous fruits this layer may remain thin-walled or may become a part of the stony endocarp, as in some species of *Prunus*, and in *Sambucus* and *Symphoricarpos*. If it remains soft, it may break down in the ripe fruit, as in some species of *Prunus* and *Cornus*.

The Fleshy Layer.—In the ovary of some fruits, the cells which later form the flesh are already formed, and growth to the mature condition does not involve cell division. Such is often the condition in berries such as those of *Ribes* (currant and gooseberry), *Berberis* (barberry), and *Vaccinium* (blueberry and cranberry). In fruits with hard endocarp this condition is rare, but occurs, for example, in *Rubus* (raspberry (Fig. 133, A, B, C) and blackberry). In forms where the development of the flesh involves the formation of many new cells, cell division occurs either in the radial or in the tangential plane, or in both these planes. It is said to be only radial in *Actaea*, *Sambucus*, and *Symphoricarpos*; only tangential in *Vitis* and *Physalis*; but in both planes in *Cucumis*, *Ligustrum*, *Cornus*, and *Asparagus*. In the development of the stony endocarp of many fruits it is probable that divisions take place, as a rule, in both planes; in *Gaylussacia*, however, the cells of the stony endocarp appear to be already present in the ovary. The rapid growth of the fleshy layer takes place largely after the growth of the seed, and, in stone fruits, after the growth of the endocarp is nearly completed. In many fleshy fruits growth is extremely rapid at the end of development, great enlargement occurring in a few days or even hours. This rapid growth consists mostly of the radial enlargement of cells and of the formation of intercellular spaces between separated cells. In partly grown fruit the cells of the developing flesh are often tangentially elongated; when ripe, these same cells become isodiametric again, or even, as in most cases of very rapid growth at the last, radially elongated. Thus ripening involves, histologically, increase in cell size and change in cell shape, the cells becoming turgid with fluid and the walls often excessively thin and delicate; it may also involve, to a greater or less extent, the separation of the cells from one another. In some cases the cells are already freed in part while the fruit is still immature (Figs. 132, A; 133, D). The dissolution of the middle lamella, which in some cases, as in *Crataegus*, is very thick, sets the cells free. The fluid filling the flesh cells is said to come in part from the breaking down of various substances, such as starch, pectic and cellulosic materials, organic acids, etc., into more soluble substances. During these ripening changes the cells and the fruit itself may not enlarge, as is the case in the apple, and the cells may even shrink in size, the intercellular spaces becoming correspondingly larger. But in many fruits, such as the cherry, blueberry, and raspberry (Fig. 133, B, C), the period of greatest growth is also that of ripening. It is probable that in all fruits the

fluids formed within the fruit, or brought in during ripening, are retained within the cells of the flesh, even when the fruit is very ripe. (The extent to which water is brought into a mature, ripe fruit seems to be in question.) A certain very small amount of free fluid coming from the dissolved middle lamellae may be present between the cells, but the apparently free fluid found on the opening of soft fruits is probably always intracellular fluid set free by the rupture of the tenuous walls of large turgid cells. Very slight pressure is sufficient to break such cells, possibly even the changes in tissue tension brought about by the breaking of the epidermis. Although there is insufficient information concerning the histological structure of ripe fleshy fruits, it seems probable that the cell walls of this tissue do not break down until decomposition sets in.

The Placenta.—In many fruits, especially those of the fleshy type, enlarged placentae form a considerable, even a large, part of the fruit, as in the tomato and watermelon. Even in some dry fruits, such as the capsule of *Epigaea*, the arbutus, the placenta is large, fleshy, and berry-like. The placenta is, of course, a part of the carpel, though not usually considered a part of the pericarp. In histological structure it is similar to the pericarp.

Accessory Fruit Parts.—The structure of fleshy fruits the flesh of which consists to a greater or less extent of parts other than carpels—such as the receptacle in the strawberry and the blackberry, the calyx in the wintergreen berry, mulberry, pineapple, etc., and of other parts in other fruits—though various in nature, is, in general, like that of other fleshy fruits. The pulp of the strawberry is said to be developed in large part by a cortical, phellogen-like meristem, which forms many cells centripetally. Inside this there is the vascular cylinder and the enlarged pith.

In fruits developed from inferior ovaries it is commonly believed that the ripened receptacle constitutes a large part of the flesh, as in the apple. Anatomical studies appear to demonstrate, however, that this is not the case. In the majority of cases the outer tissues of an inferior ovary consist of the "calyx tube," which is adherent to the carpels. Morphologically, the calyx tube in such cases is made up of the fused bases of petals, stamens, and sepals. Thus the pericarp in such fruits is morphologically very complex. However, the larger part appears to represent the tissues of the calyx. This is especially true in the Rosaceae (apple, pear, and quince), and the Ericaceae (blueberry, huckleberry, and cranberry). Thus the outer flesh of the pome fruits is doubtless largely calyx in nature, and only a small part of the fruit of this type is receptacle morphologically. The pulp of citrus fruits is of different nature from that of most fruits, since it consists of hairs developed from the inner epidermis of the carpels, which become turgid with fluid and fill the ovarian cavity. Somewhat similar fleshy hairs occur externally in some species of *Rhus*

(sumach) and in other genera. In another type of fruit, the fleshy parts are the outer layers of the seed coats, as in *Punica* (pomegranate).

Dehiscence.—Comparatively little appears to be known of the anatomical basis of dehiscence. In many cases there seems to be little or no histological determination of the place of dehiscence, opening occurring along “sutures,” which are normal lines of structural weakness. In other cases a line of separation is determined by the development of rows of special cells weakly held together, separation later occurring between these rows by the tearing apart of the tissues upon changes in tissue tension due to drying or ripening. The development and specialization of these opening cells accompanies that of the cells of the rest of the fruit and does not follow at a much later period as does the development of absciss layers in leaves and stems. Dehiscence is apparently not commonly due, as is abscission, to the separation of individual cells, or to the disintegration of tissue. The stress brought about by unequal growth or by unequal drying out of the pericarp may cause sudden and even explosive rupture of the fruit along lines of weakness.

THE SEED

The enlarged and matured ovule with the included embryo constitutes the seed. To a large extent the structure of the ovule is maintained in the seed, just as is that of the ovary in the fruit. The general conformation is retained, and the external morphology and orientation are often readily visible. The integuments, or parts of them, together, in some cases, with the nucellus, are well developed and surround the embryo and endosperm. The simplicity of histological structure found in the ovule is continued in the endosperm and embryo, but is replaced in the seed coats by marked complexity.

The Seed Coats. *Morphology.*—Throughout the different groups of seed plants the ovule has either one or two integuments. In the dicotyledons the majority of the Gamopetalae and Apetalae and some Polypetalae have but one integument, as do some of the monocotyledons; other angiosperms have two integuments. Sometimes the entire integument, or integuments, enters into the composition of the seed coat. More often, however, the seed coats are developed from a part only of the integuments, other parts being absorbed as the seed develops. When such absorption takes place, it is the innermost or sometimes the median layers of an integument which are removed. Further, whether the integuments develop as a whole or in part, the nucellus may contribute to the seed coats, becoming distinguishable only with difficulty from the adjacent inner layers of the integument (Fig. 134, *D*). However, in probably the majority of cases the nucellus is wholly absorbed and is not represented in the seed. The reduction of the tegumentary tissues

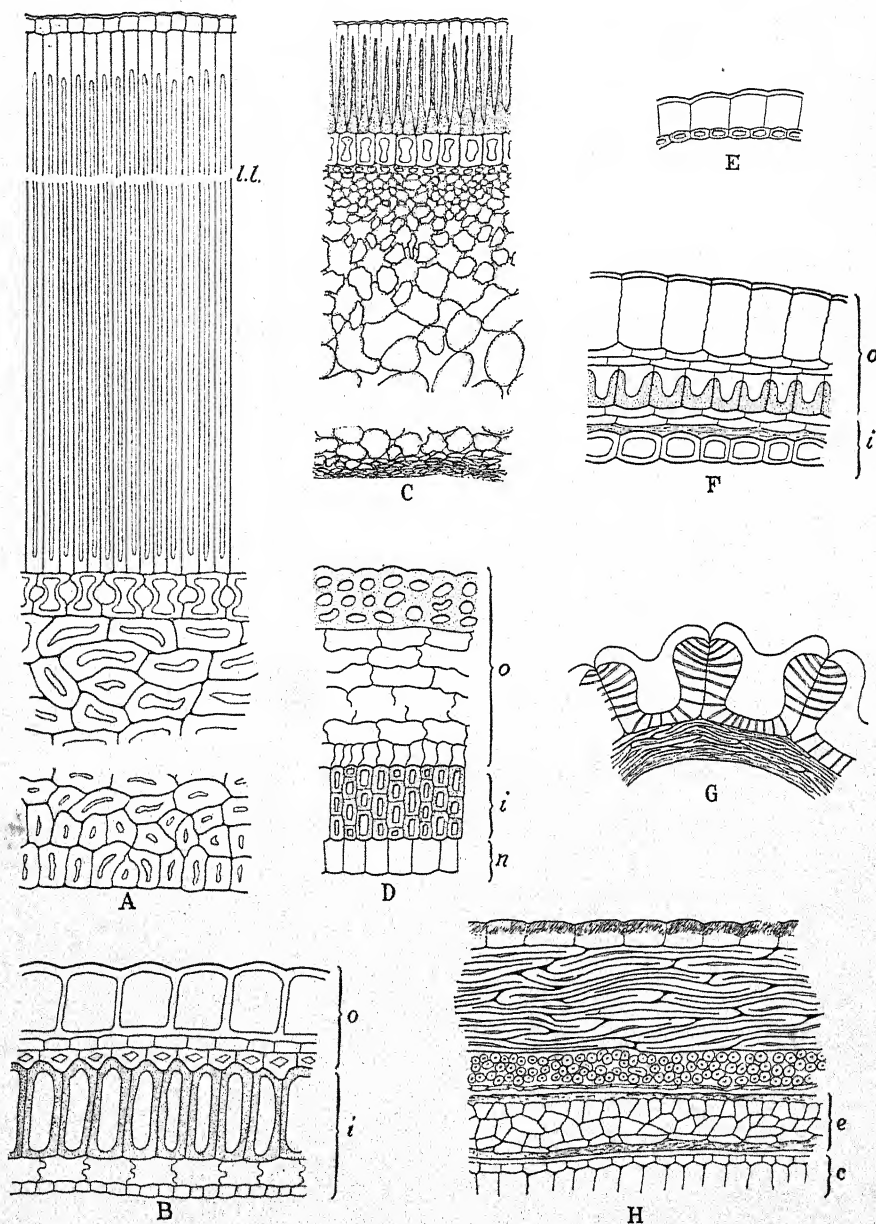


FIG. 134.—Seed coats. A, *Gymnocladus dioica* (only one-fifth of the stony endocarp shown). B, *Viola tricolor*. C, *Phaseolus multiflorus* (only one-third of the soft endocarp shown). D, *Magnolia macrophylla*, the exocarp (only shown in part) fleshy. E, *Plantago lanceolata*. F, *Lepidium sativum*. G, *Vaccinium corymbosum*, the epidermal cells very large, with heavy inner, and delicate, outer walls. H, *Pyrus Malus*. c, cotyledon; e, endosperm; i, inner integument; l l, "light line;" n, nucellus; o, outer integument. (B, D, E, F, after Brandza.)

goes very far in some cases, chiefly in indehiscent fruits where only the two or three outer layers—sometimes only the outer epidermis—of the outer integument persist in the ripe seed, as in the Umbelliferae. In the Compositae the extreme of reduction has occurred, for the integuments have entirely disappeared in the ripe seed, as have also the inner layers of the pericarp, so that the fruit is an achene in which the seed and the fruit tissues are intimately associated and not readily separable.

Where there are two integuments in the ovule, various different conditions exist in the seed. Both integuments may be present in the seed coat, the inner represented by all its cell layers, the outer by all or by only the outermost two or three layers. Here the inner integument forms the important part of the seed coat, its outer part forming the protective layer (Fig. 134, *B*). This condition is found in the Malvaceae, Tiliaceae, Violaceae, Hypericaceae, etc. Again, where both ovule coats are present, the outer is strongly developed, with protective layers, and the inner, though several-layered, is rather unspecialized (Fig. 134, *F*). Of such structure are the seed coats of the Cruciferae, Berberidaceae, Papaveraceae, and certain lilies, irises, and aroids. In the Onagraceae, Lythraceae, Aristolochiaceae, etc., both integuments form lignified protective layers and at least the outer layers of the nucellus contribute to the seed coats. In the Magnoliaceae the inner integument becomes the protective seed coat and a part of the nucellus is attached to it; the outer integument often becomes fleshy (Fig. 134, *D*). Complete absorption of the inner integument and of the nucellus occurs in the Ranunculaceae, Leguminosae, and in certain lilies and amaryllises.

In ovules with one integument, only rarely does the entire structure become seed coat, a larger or smaller inner or median part being usually absorbed. Thus the outer layers together with the inner epidermis of the integument form the seed coat, as in the Polemoniaceae, Plantaginaceae (Fig. 134, *E*), Balsaminaceae, etc. In most plants with one ovule integument the nucellus does not contribute to the seed coats; but in the Linaceae a well-developed nucellus is added to a weak integument, the median layers of the nucellus disappear, and the epidermis of the nucellus becomes the protective layer. So various and so obscure is the morphological nature of seed coats that in most cases this can only be determined by ontogenetic studies.

Histological Structure.—Regardless of the morphological nature of the seed coats, these structures, except in dry indehiscent fruits, are histologically complex. They are characteristically made up of fairly distinct layers of different types of cells. Commonly on the outside, or near the outside, there is a layer of thick-walled, lignified or cutinized protective cells. The innermost layers, or in some cases the median layers, often consist of thin-walled parenchyma cells which, while the

seed is developing, are filled with food materials. These cells are represented in the mature seed by papery layers of empty, collapsed cells, the contents having been used in the nourishment either of the specialized layers of the integuments or of the endosperm and embryo. Between these layers and the heavy-walled protective layer, or sometimes external to the latter are other layers of various thickness, and of many kinds of cells. Among these are stone cells of many types, fibers, parenchyma cells of the greatest variety, both in size and shape, in content, and in nature of the wall. The successive layers are typically made up of cells of very different kinds, and often the cells of adjacent layers are differently oriented, the long axes being vertical in one and horizontal in another, or extending longitudinally about the seed in one case and transversely in the other (Fig. 134, *H*). Cells with peculiarly and irregularly thickened walls are common (Fig. 134, *F*, *G*), as are those of remarkable shape and unusual relation to adjacent cells. Mucilaginous cell walls are of frequent occurrence, especially where the protective cells lie one or more layers below the surface. In such cases there is no cuticle. Commonly, however, a well-defined cuticle is present, especially in the harder types of seeds, such as those of many of the Leguminosae (Fig. 134, *A*, *C*), in *Canna*, *Ceanothus*, etc. The scarification of seeds and the treatment with sulfuric acid to increase the percentage of germination are based in large part upon the necessity of rupture or destruction of the cuticle to permit the entrance of water and oxygen. Some seeds have the outer layers of the seed coats fleshy—those with the seeds exposed at maturity, such as those of *Magnolia*, *Celastrus*, *Caulophyllum*, and *Ginkgo*, are histologically similar to fleshy fruits; those not exposed, such as those of *Lycopersicum* (tomato), *Passiflora* (passion fruit), and *Punica* (pomegranate), are less complex in the outer layers. The protective layer, present in most seeds, is made up characteristically of close-packed, radially placed, and heavy-walled columnar cells. This layer is often called the palisade layer, and its peculiar cells are sometimes referred to as "Malpighian cells" (because first described by Malpighi). The palisade layer of seeds much resembles, in arrangement of cells, in variety of layers, etc., the palisade layer of leaves. It is, however, very different in being a sclerenchymatous layer without intercellular spaces. The walls are commonly unevenly thickened (Fig. 134, *C*, *F*, *G*); they may be of cellulose or be heavily cutinized or lignified. Functionally, they doubtless serve as a protection both against mechanical injury and against changes in water content in the seed. The palisade layer nearly always shows a "light line," a band-like region running transversely to the long diameter of the cells—and hence tangentially in the seed (Fig. 134, *A*)—where light refraction is different from that in the rest of the cells, and where the cell wall is chemically and physically modified in some way apparently not well understood.

The Vascular Bundles of Seeds.—The bundles of seeds are inconspicuous, and in seeds developed from orthotropous and campylotropous ovules are very short or lacking. The strands lie only in tissues developed from the outer integument and extend to the chalazal region, or in some cases reach beyond, around the ovule even to the micropylar region. In rare cases two bundles enter the base of an ovule; where this occurs the ovule is usually basal and appears to possess in addition to its normal supply the vascular supply of an adjacent ovule lost in evolutionary development. The bundles are small, mostly amphicribal, the elements few, the xylem of protoxylem, and the phloem usually without sieve tubes. There is a marked tendency for these bundles to turn and twist in their course.

Embryo and Endosperm.—The embryo consists largely of thin-walled parenchyma, in considerable part meristematic; in the cotyledons, however, the cells in many cases are mature. These cells are rounded or polyhedral, always with intercellular spaces, and often packed with starch or aleurone. The mesophyll, like that of typical leaves, may show palisade and spongy layers. The epidermis is simple and is without stomata where the cotyledons are thick and do not expand on germination. Such cotyledons contain starch, whereas the thin, leaf-like ones contain aleurone and possess stomata. The vascular tissue is usually in the procambium stage; only rarely are protoxylem and proto-phloem elements mature, as in *Quercus*, *Aesculus*, and *Castanea*. The venation of the cotyledons varies with the plant, but in thick cotyledons the vascular supply is much simplified.

The endosperm consists always of polyhedral parenchyma cells more or less isodiametric in shape. The walls are largely cellulose and commonly thin, but in some plants, such as the date (*Phoenix*) and the persimmon (*Diospyros*—Fig. 12, *E*, *B*), are greatly thickened, the additional cellulose being reserve food. Such endosperm is very hard and is commonly known as "horny" endosperm. The storage materials in typical endosperm are starch, aleurone and oils; starch and aleurone, it is said, do not occur in the same cell.

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CHAPTER XIV

ECOLOGICAL ANATOMY

In the foregoing chapters emphasis has been placed upon normal plant structure as it is developed in regions of average or optimum water supply. Such an environment is characterized as *mesophytic*, and is that which obtains generally in the important agricultural districts of the temperate zone and also in parts of the tropics, especially at the median altitudes. The plants which have developed in this environment are known as *mesophytes*, and include the majority of the best-known wild and cultivated plants of temperate regions.

In the course of evolution plants have become adapted in structural and physiological features to life under conditions which are extreme as regards water relations. There is thus an extensive flora of vascular plants, known as *hydrophytes*, which live upon the surface of bodies of water or submersed at various depths down to those where diminished light intensity and possibly pressure become limiting factors for the growth of plants of this type. Much greater in number of species and more diversified in structural complexity is the great group of plants adapted to growth in regions where the supply of available water is deficient, that is, in a so-called *xerophytic* environment. This group, known as *xerophytes*, includes species from many families in no way closely related phylogenetically, which, under influence of a similar environment, have come to resemble each other more or less closely in vegetative characters. Between the extreme xerophytes and the hydrophytes are to be found all gradations of form and all degrees of structural adaptation occurring in plants whose natural habitat is intermediate between mesophytic and xerophytic on the one hand and mesophytic and hydrophytic upon the other.

Types of Xerophytic Environment.—The structural modifications common to xerophytes have been evolved under many different environmental conditions, and this has led to the recognition of several types of xerophytic situations. The most common of these is that found in deserts or semi-arid places where there is actually a deficiency of rainfall during either a large part or all of the year. Here are found many plants, not typically xerophytic in structure, which grow only during a short rainy season and pass the dry season as seeds, or as dormant bulbs, corms, or roots beneath the surface of the ground. In such locations there are also, however, with the exception of extreme deserts where no higher

plants can grow, a considerable number of species which maintain stems and leaves, or only stems, above ground during the whole year, and these must, of necessity, be effectively protected against water loss. In addition to these situations characterized by actual lack of water are those environments where water is apparently abundant, but is for some reason physiologically unavailable to the plant. Thus there is recognized a group of plants, known as *halophytes*, which grow in salt marshes or in certain types of alkali soil which are only slightly toxic. These plants, although frequently standing in water, have elaborate structural modifications to prevent water loss, much like those found in plants of the desert flora. In this case the water, though present, is of such high osmotic concentration that it cannot be readily absorbed by the plant; or as a result of its toxicity, the root system is dwarfed. A somewhat similar condition is found in the peat bogs of the colder temperate and the subarctic regions where the water is not absorbed, not because its concentration is osmotically too high, but probably because of a toxic effect upon the roots of the plant which hinders their development, or because of the very low temperature of the soil. In any case, typical xerophytic structures are found in plants growing in this type of situation.

Another set of conditions which is physiologically xerophytic is that found in regions where there is no actual lack of water, but which are cold for a part of the year. Here the low temperatures greatly cut down the rate of absorption by the roots, and reduce conduction generally, so that even if transpiration is also reduced there is a physiological shortage of water. This situation is particularly true where the soil freezes to a considerable depth. Plants which hold their leaves under such conditions show typical xerophytic structure, as, for example, the many species of needle-leaved gymnosperms which are generally distributed in the temperate and subarctic zones.

Exposure to persistent winds of high velocity and to intense light and heat also has the effect of a xerophytic environment upon plant life. Many xerophytic situations are the result of a combination of the environmental factors described above. Thus, in a desert situation, lack of moisture, both in soil and atmosphere, intense light and heat, and winds of high velocity may be operative.

Structural Adaptation to Xerophytic Conditions.—The ways in which plants have become modified to meet xerophytic conditions are many and varied and are of two general classes, physiological and structural. In the former category are those in which the normal mesophytic organs and tissues have not been changed in structure, but have become physiologically more effective, such as is the case with plants growing in dry situations, which develop an extraordinarily large and deeply penetrating root system capable of efficient absorption, as does, for example, the olive. Another example of this kind of modification is found in those salt-marsh

plants which have a higher osmotic concentration within the plant than is found in the common mesophytes, thus enabling them to take up water from the soil solution. With this high osmotic concentration is coupled the ability of the plant cells to resist the toxic action of the salt solution, which would undoubtedly be injurious to many other types of plants. The presence of colloids in high concentration, increased concentration of gases, and other similar conditions are of this sort. Along with such physiological adaptations are also commonly found structural modifications to prevent water loss from the plant when it is once absorbed; and it is with these that this chapter is primarily concerned. Some of the structural specializations found are of great intricacy and may involve nearly all of the tissues of the plant. In the majority of cases a number of different means are employed by the same plant to prevent water loss.

Lignification and Cutinization.—Among the most common of xerophytic modifications is heavy cuticularization, and extreme cutinization of the epidermis and even of subepidermal cells. All gradations are found in the degree of cuticularization from the formation of a cuticle only slightly thicker than normal, as is found frequently upon plants of semi-xerophytic conditions, to the elaborate thickenings of extreme xerophytes in which the cuticle may be as thick as or thicker than the diameter of the epidermal cells. Frequently, the walls of the epidermal cells themselves are cutinized, and sometimes those of the underlying cells also. Along with well-developed cutin layers are frequently found different degrees of lignification of the cells of the epidermis and those immediately beneath this layer. In some forms, as, for example, the leaves of *Cycas*, lignification may even extend to parts of the palisade parenchyma cells (Fig. 135, C). Similar to cuticularization is the formation of wax as a protective covering on the epidermis. Many plants secrete wax externally in small amounts, but certain genera, as, for example, *Copernicia* and *Ceroxylon*, the sources of carnauba wax, produce this substance in quantities sufficient to be commercially valuable. Wax is sometimes produced by plants not growing under xerophytic conditions.

The Hypodermis.—As an additional protection, many xerophytic plants possess one or several layers of cells immediately beneath the epidermis which function in the same way. This layer is frequently designated as the *hypodermis* (Figs. 135, C; 138, A, B). Its cells are often much like the epidermal cells in structure, and in rare cases may be derived in ontogeny from the young epidermis. In most cases, however, the hypodermis of leaves is morphologically mesophyll, and may be in the form of a layer of stone cells, or a sheet of fibrous tissue. Water-storage tissue of leaves is often of hypodermal position. The hypodermis of stems belongs to the outer cortex. Whereas a hypodermis in stems, collenchymatous or sclerenchymatous, is usually a feature of mesophytic structure (though a hypodermis of collenchyma is often found in the stem

of aquatic plants, as in *Trapa*), a hypodermis in leaves is characteristic of xerophytes. The hypodermis of leaves may be cutinized to some extent, or, as is more frequently the case, may be lignified. Gums and tannins are common in this layer (Fig. 136, A).

Sclerenchyma.—In addition to the hypodermis, xerophytes generally have a larger proportion of sclerenchyma in their leaf structure than is found in normal mesophytes. This tissue, as masses either of fibers or stone cells, is usually arranged in more or less regular layers between the mesophyll of the leaf and the epidermis or hypodermis. In some plants,

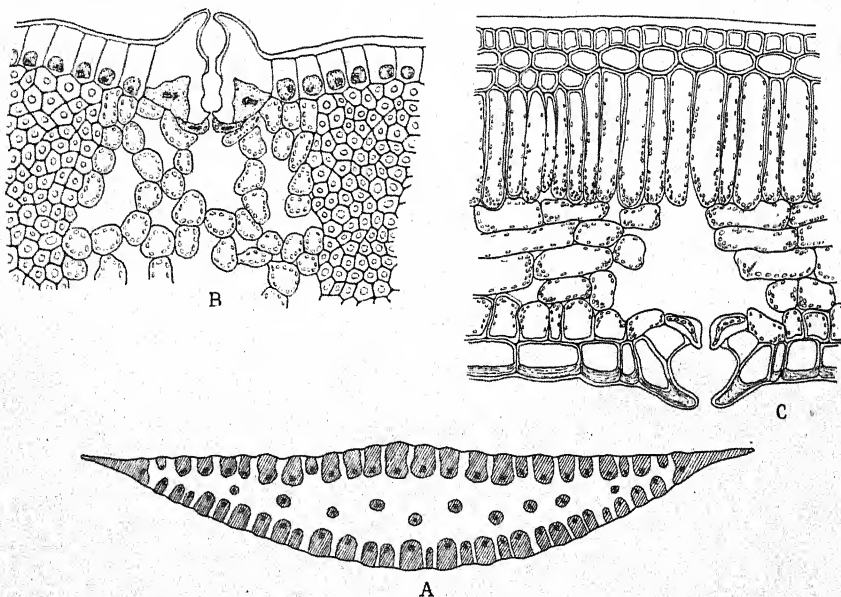


FIG. 135.—Structure of xerophytes; leaves. A, diagram of cross section, *Dasylirion serratifolium*, sclerenchyma singly cross-hatched, vascular tissue doubly cross-hatched. B, detail of small marginal portion. C, cross section, *Cycas*; showing lignified hypodermis and partly lignified palisade tissue.

as in *Banksia* (Fig. 136, A), there is a continuous, rather thin sheet of sclerenchyma next the hypodermis and covering the mesophyll tissues. In other forms, as, for example, in *Dasylirion* (Fig. 135, A, B), there are heavy, parallel strands of fibers next the epidermis of the leaf. These strands cover the mesophyll except for small openings leading from the stomata to the interior of the leaf. In addition to offering some protection against water loss, such sclerenchyma layers, of course, function in the support of the organ, and may also act as a partial screen against intense light. Xerophytes which rely chiefly upon increased cutinization and sclerification of the leaves for protection are commonly designated as *sclerophyllous*.

Epidermal Hairs.—The modifications so far described have functioned to prevent water loss from the plant by the formation of protective layers which are themselves more or less impervious to water. Another type of protection is effected by the cutting down of the circulation of air over the leaf surface and the prevention thereby of rapid evaporation through the stomata. This result is brought about in many plants,

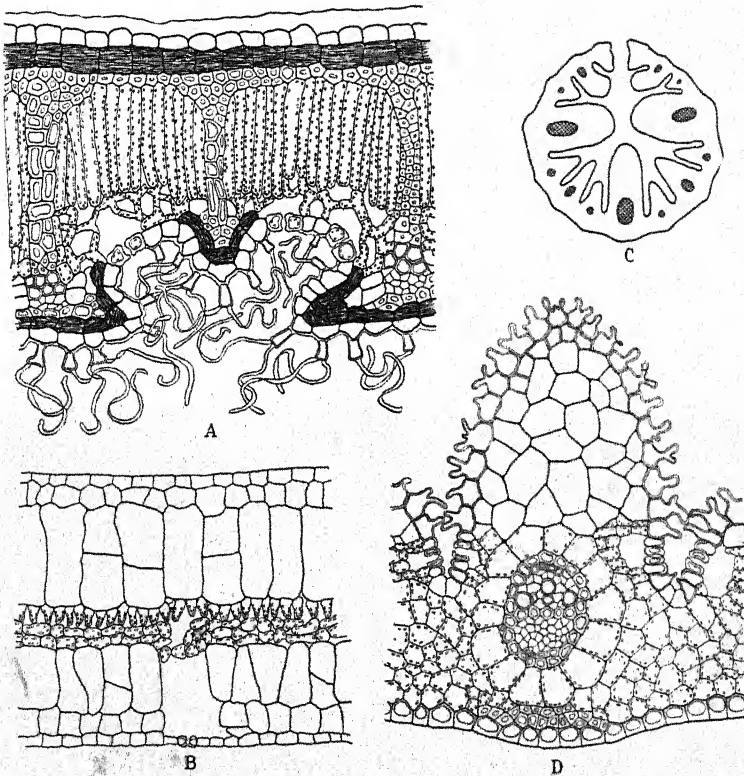


FIG. 136.—Structure of xerophytes; leaves. A, a sclerophyllous type, *Banksia*. B, a malacophyllous type, *Begonia*. C, D, leaf adapted to rolling, *Spartina*. A, an extreme type with very thick cuticle, outer hypodermal layer filled with mucilage and tannin, mesophyll pockets enclosed in sclerenchyma, stomata in hair-filled pockets, spongy parenchyma sparse. B, mesophyll thin, protected by layers of mucilage-containing cells, stomata unprotected. C, diagram of cross section of leaf in rolled condition. D, detail of portion of same; stomata in furrows nearly closed by interlocking epidermal cells.

especially those of alpine regions exposed to strong winds, by the production of a covering of matted hairs on the under side of the leaves, or wherever stomata are abundant. Hairs may also be abundant over the entire aerial part of the plant. The types of hairs are numerous: long and simple, appressed or matted; stellate or otherwise branched; scale-like or peltate. In each case they form a dead-air space next the leaf epidermis where air is maintained at a relative humidity approach-

ing that on the inside of the leaf. The types of hairs, though showing great diversity, are often constant for a genus and even for larger groups. Xerophytes which depend largely upon the hairy covering of the leaves and stems for protection against drying are known as *trichophyllous*.

Rolling of Leaves.—A considerable number of xerophytes, of which the xerophytic grasses are the outstanding example, prevent rapid loss of water by the rolling of the leaves. In the leaves of such plants the stomata are located upon the upper or ventral surface only, so that when the edges of the leaf roll inward, or turn upward and fold inward until the edges touch, the stomata are very effectively shut away from the outside air. An extreme example of this kind is seen in *Spartina*, a salt-marsh grass, which, in addition to having the leaf tightly folded, has the stomata further protected by placement in deep furrows or grooves (Fig. 136, C, D). As brought out in Chapter XII, the leaves of many grasses are adapted to rolling up by the presence of special motor cells upon the upper surface. In the xerophytic grasses these cells are particularly well developed. Other linear-leaved plants, as, for example, species of *Dasylyrion*, possess leaves capable of rolling; and with certain broad-leaved forms the same result is effected by the folding of the leaves under conditions of deficient moisture.

Xerophytic Stomatal Structure.—Since the stomata are the channels through which water vapor normally escapes from the plant, modifications of the stomatal apparatus for the conservation of moisture under xerophytic conditions are to be expected. The rôle of transpiration is coming to be looked upon as not in itself of benefit to the plant, but as a phenomenon which is the inevitable result of the maintenance of the conditions necessary for photosynthesis. A supply of water is necessary in the leaf to maintain cell turgor and keep the cell membranes moist so that they may be efficient in the absorption of gases. The stomata are necessary for the intake of carbon dioxide and oxygen and possibly for the passage inward and outward of other gases. The opening of the stomata permits the escape of water even under conditions in which water loss is harmful to the plant as a whole. Thus the reduction of transpiration is of the utmost importance among xerophytes, and is frequently brought about both by the reduction of the number of stomata, either by reduced leaf surface or smaller number per unit area, and by elaborate modification of the structure of the stomatal apparatus. In addition to the protection afforded stomata by the presence of hairy coverings and by the rolling or folding of leaves, it is common in xerophytes to find these openings much sunken below the level of the other epidermal cells. In these cases the accessory cells may be of such shape and arrangement as to form one or more outer chambers connected by narrow openings with the stoma itself. Thus the opening between the guard cells is protected from contact with the outside air and consequently

from air of low humidity. Stomata of this type are common in the extreme xerophytes, as, for example, in *Pinus* (Fig. 138, B, C), *Equisetum* (Fig. 138, D), *Cycas* (Fig. 135, C), and *Leptocarpus* (Fig. 137, B). The walls of the accessory cells in such cases are ordinarily very thick and heavily lignified or cutinized, as are frequently also parts of the walls of

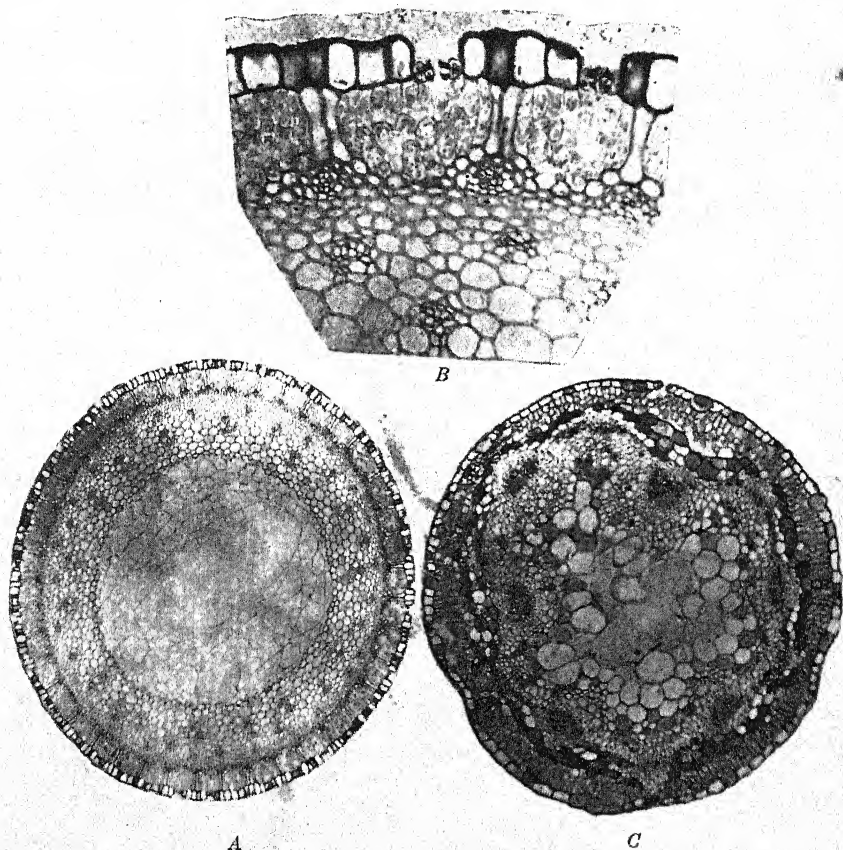


FIG. 137.—Structure of xerophytes; microphyllous types. A, B, *Leptocarpus*, monocotyledon; A, cross section of stem, B, small portion of A; showing specialized cortical photosynthetic tissue, sunken stomata, lignified epidermis; the leaves, non-functioning scales, appearing in section outside epidermis in B. C, *Polygonella*, cross section of stem, showing similar condition in dicotyledon.

the guard cells. Further protection may be given to sunken stomata by hairs, as in *Casuarina* and *Banksia* (Fig. 136, A).

Reduced Leaf Surface.—One of the larger groups of xerophytes is made up of the so-called *microphyllous* forms. Here water loss is partly prevented by the reduction of the leaf surface so that the total exposed surface of the plant body is relatively small as compared with that of normal mesophytes. Abundant illustrations of this type of xerophyte

occur in all groups of plants, for example, *Equisetum*, *Thuja*, *Pinus*, *Casuarina*, *Asparagus*, the cacti, *Polygonella* (Fig. 137, C), etc. In these forms the leaves, if normal in function, are very small; often they are wanting in the mature plant, or persist as small scales or bracts which are for the most part devoid of the usual functions of leaves. In such cases the normal leaf function of photosynthesis is taken over by the stem in which photosynthetic tissues are well developed, as in *Equisetum*, *Leptocarpus*, and *Polygonella*. The reduction of leaf surface is commonly combined with other xerophytic adaptations, such as increased sclerenchyma, sunken stomata, water storage, etc.

✓ *Fleshy Xerophytes*.—A fourth large group of xerophytes includes those possessing fleshy leaves or stems, and designated as *malacophyllous*. In these forms there may not be well-developed structures for the prevention of water loss, but rather the presence of tissues adapted to the storage of water or mucilaginous substances. In leaves these tissues may be located beneath the upper or the lower epidermis, upon both sides of the leaf, or, in extreme types, in the center also. The origin of the water-storage tissues may be either epidermal or cortical. The cells are usually very large and are sometimes thin-walled, as in *Begonia* (Fig. 136, B). Frequently, however, the walls are reinforced to prevent collapse when turgor is reduced. Such storage tissue may actually be used as a source of reserve water during drought, or may serve to protect the underlying tissues against excessive light. The thickened leaves of this type of plant tend to be terete in form, with the vascular bundles arranged in a stele-like cylinder. *The mesophyll, consisting frequently of a large proportion of palisade tissue, is more compact than is the case in mesophytes, and the amount of photosynthetic tissues is greater relative to the amount of leaf surface exposed. Thus, there is a proportionately reduced leaf surface. Frequently, the stems of microphyllous xerophytes are provided with water-storage tissues, as, for example, some of the cacti and other plants of similar habit, and certain salt-marsh plants like *Salicornia*.

Mucilages and gums of various sorts are found in malacophyllous plants generally. These, by their colloidal nature, together with the organization of the living plant, are apparently effective in holding water under extreme conditions of drought. Possibly, the effect of the mucilage or gum has been overemphasized, since these substances, when removed from the plant, dry with considerable rapidity. It is true, however, that many plants with fleshy leaves or stems which contain mucilaginous substances are extremely resistant to desiccation, as, for example, species of *Sedum* and *Opuntia*.

✓ The importance of intense light as a factor contributing to xerophytic conditions is not fully understood. In alpine situations where the ultra-violet rays are strong and in desert regions where there is much reflection

from the sand, light may be directly injurious to the protoplasm of the plant. Light may also increase transpiration and thus under xerophytic conditions may be indirectly injurious by causing water loss. The shielding of the mesophyll from these severe conditions may be accomplished by the presence of a masking layer of sclerenchymatous or water-storage tissue, a white or gray epidermal surface which reflects light, or dense layers of palisade tissue with the cells much elongated. The chloroplasts arranged along the walls of these elongated palisade layers receive the direct light rays upon their edges only. Some plants, often called "compass plants," as, for example, species of *Lactuca*, have their leaf blades so oriented that they expose only their edges to the direct rays of the sun, thus shielding the photosynthetic tissues. All these modifications may, of course, function in other ways as adaptations to a dry environment, so that the effect of light alone is difficult to determine. The direct effect of light upon the development of the mesophyll of leaves is readily seen in plants of mesophytic structure. Thus in the same species, leaves grown in full sunlight may have two or three dense rows of palisade cells, those developed in light of less intensity a single loose palisade layer only, and those grown in deep shade may lack palisade tissue altogether.

Needle Leaves of the Gymnosperms.—A special type of xerophily is found in the needle leaves of the gymnosperms. Here, in some species, the xerophytic structures are an adaptation to an environment actually deficient in water. In the majority of cases, however, as with many species of *Pinus* and *Picea*, the plants are exposed to xerophytic conditions only during the winter when low soil and air temperatures prevent water absorption and conduction, and do not entirely inhibit water loss from the leaves. In these leaves the xerophytic adaptations are chiefly those of reduced leaf surface, heavy cutinization, and sunken stomata. The characteristic structures are well shown in the leaf of *Pinus Laricio* (Fig. 138, A-C). Here the vascular tissues consist of two collateral bundles each made up of about equal amounts of xylem and phloem, which are largely secondary in origin. Immediately surrounding the vascular tissues is a zone of so-called transfusion tissue (p. 76) limited by a well-defined endodermis. Some of the cells of the transfusion tissue, which is of pericyclic position, show bordered pits even though the tissue has otherwise the appearance of parenchyma. Exterior to the endodermis is the photosynthetic tissue, which is made up of a special type of mesophyll cells. In these cells the inward projections of the wall greatly increase the wall surface upon which the chloroplasts may be distributed. The walls of the epidermal cells are cutinized upon the outer surface, the cutinization extending along the middle lamellae between and around the cells. The wall is thickened to such an extent that the lumen of the cells is practically occluded with lignified material. Beneath the epi-

dermis is a well-developed hypodermis several layers thick, consisting of elongate sclerenchyma cells extending parallel with the long axis of the leaf. The stomata are somewhat sunken and arranged in definite longitudinal rows. Their structure as seen in transverse and longitudinal sections of the leaf is shown in Fig. 138, *B, C*. The needle leaves of other gymnosperms, though differing in structure from those of *Pinus* just described, are for the most part similar in general features.

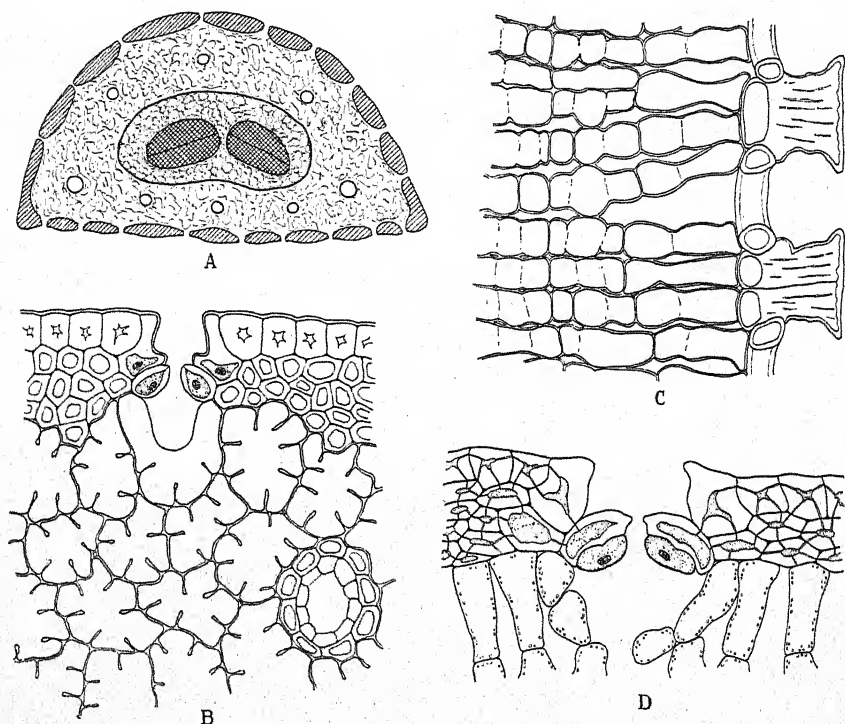


FIG. 138.—Structure of xerophytes; microphyllous types. *A, B, C*, leaf of *Pinus Laricio*, diagram of cross section, detail of small part of same, and of small part of longitudinal section through stomatal furrow, respectively. *A*, the two vascular bundles, doubly cross-hatched, surrounded by parenchyma sheath and endodermis; the mesophyll with resin canals, protected by external sclerenchyma, singly cross-hatched, broken by stomatal furrows. *B, C*, the mesophyll uniform, dense, with infolded cell walls. *D*, detail of outer portion of cross section of stem, *Equisetum hyemale*, showing cortical photosynthetic tissue, sunken stoma, heavily silicified epidermis and hypodermis.

Epiphytes.—In many situations, particularly in tropical and subtropical regions, there are species adapted to growth upon other plants and other supports rather than in the soil. Such plants, usually known as epiphytes, do not form any structural connection with the plant upon which they are growing, as do parasites with their host, but merely use the larger plant as a support. With epiphytes, water is obtained directly from rains or moist atmosphere, and mineral nutrients apparently from

the decaying bark of the trees upon which the plants may be situated, or from dust and organic matter which lodges about the plant. In rain forests there may be collected about the plant a very considerable amount of vegetable detritus made up of mosses, lichens, leaves, bark, and other material. Thus the epiphyte may have a considerable amount of soil at its disposal. Many orchids and other monocotyledons, certain ferns, such as the staghorn fern, *Platynerium*, and other plants are examples of this type of plant. The Spanish moss, *Tillandsia*, on the other hand, is able to exist with very little mineral matter and may even grow on telegraph wires and wire fences, possibly obtaining some minerals from dust blown through the air.

The structural modifications of epiphytes vary according to the special type of situation to which they are adapted. Many are xerophytic in their general structure, as, for example, *Tillandsia* and a considerable number of orchids, the former having a hairy covering and the latter heavily cutinized epidermis and relatively small leaf surface. It is probable that some orchids are partly "saprophytic." The root system of epiphytes may consist partly of holdfasts, which anchor the plant, in part of absorbing fibrous roots which are in contact with the substratum, and in some cases of aerial roots. These aerial roots, as, for example, in *Dendrobium*, are large and covered with a thick, water-absorbing layer known as the *velamen*. Such a structure is apparently adapted to the absorption of water from the air, or for soaking up and holding rain. Not all epiphytes show xerophytic structure, as some situations are always moist, so that there is not even temporary exposure to drought.

Hydrophytes.—The group of vascular plants which naturally grow submersed in water, or floating, is much smaller in number of species and displays much less varied structural adaptation than do the xerophytes just discussed. This is probably due to the fact that aquatic environments everywhere show great uniformity, whereas the factors which determine xerophytic habitats are many and varied. The factors affecting the aquatic situation are chiefly those of temperature, osmotic concentration, and toxicity, the last two dependent upon the amount and the nature of the substances in solution. Under some conditions light intensity and pressure may be of importance. These factors are not subject to quick variation, and are in sharp contrast with the rapid changes and extreme conditions experienced by xerophytes. The structural changes in aquatic plants which can be considered as adaptations to environment are therefore mainly those of reduction of the protecting, supporting, and conducting tissues, and frequently the provision for aëration of the tissues by the presence of air chambers. The presence of abundant water supply, partly or completely surrounding the plant body, renders protection against loss of water and provision for water conduction unnecessary;

the buoyant effect of the water replaces mechanical support in large measure. A striking illustration of the effectiveness of xerophytic structure against drying out as contrasted with the lack of protection found in hydrophytes may be had by exposing a xerophyte, such as *Sedum*, and a hydrophyte, such as *Potamogeton*, to drying conditions. The former will remain alive for many days, whereas the latter will become dry in a very few hours.

Modifications of the Epidermis in Hydrophytes.—Possibly the most outstanding adaptation of plants generally to hydrophytic conditions is the change in the structure and the function of the epidermis as compared with plants in an aerial habitat. Thus in aquatics the epidermis, instead of being protective in function, is modified for the absorption of gases and nutrients directly from the water. This layer in the typical hydrophyte lacks cutin altogether and the thin cellulose walls permit ready absorption from the surrounding water. Commonly in aquatics, the epidermis contains chloroplasts and may thus form a considerable part of the photosynthetic tissue, especially where the leaves are very thin, as is frequently the case. Stomata are wanting in submersed hydrophytes (though sometimes vestigial), the gaseous interchange taking place directly through the cell walls. The floating leaves of aquatic plants have abundant stomata upon the upper surface.

✓ *Divided Leaves.*—In many species of aquatic plants the submerged leaves are very finely divided so that there is a proportionately much increased leaf surface in contact with the water. The slender terete segments of such leaves allow for very close contact between photosynthetic tissues and the water. Such plants as *Myriophyllum* and *Utricularia* are examples of aquatics with divided leaves of this type. Some species with divided submerged leaves have floating or aerial leaves which are entire, toothed, or lobed. The finely divided leaves of these plants suggest the analogous condition in the gills of fish where there is a large surface in contact with the water from which gases are absorbed, and it has been suggested that such leaves are an adaptation serving the same function. However, it is not impossible that divided leaves in aquatics may have developed in response to mechanical stresses or other factors rather than as absorbing organs.

Air Chambers.—Chambers and passages filled with gases are of common occurrence in the leaves and stems of submersed plants. Water-storage cavities are structurally single cells, but air chambers are definite, usually regular, intercellular spaces extending through the leaf and often for long distances through the stem. Good examples of this type of structure are found in the leaves of *Potamogeton* (Fig. 139, D, C) and *Pontederia* (Fig. 140, A). As is shown in the figures, such spaces are usually separated by partitions of photosynthetic tissue only one or two cells thick. They provide for a sort of internal atmosphere for the plant.

In these spaces the oxygen given off in photosynthesis is apparently stored, to be used again in respiration, and the carbon dioxide from respiration is held and used in photosynthesis. Projecting into these air passages of the stems, petioles, and leaf blades in some genera, as, for example, in *Nuphar*, are found special types of sclerenchyma cells some-

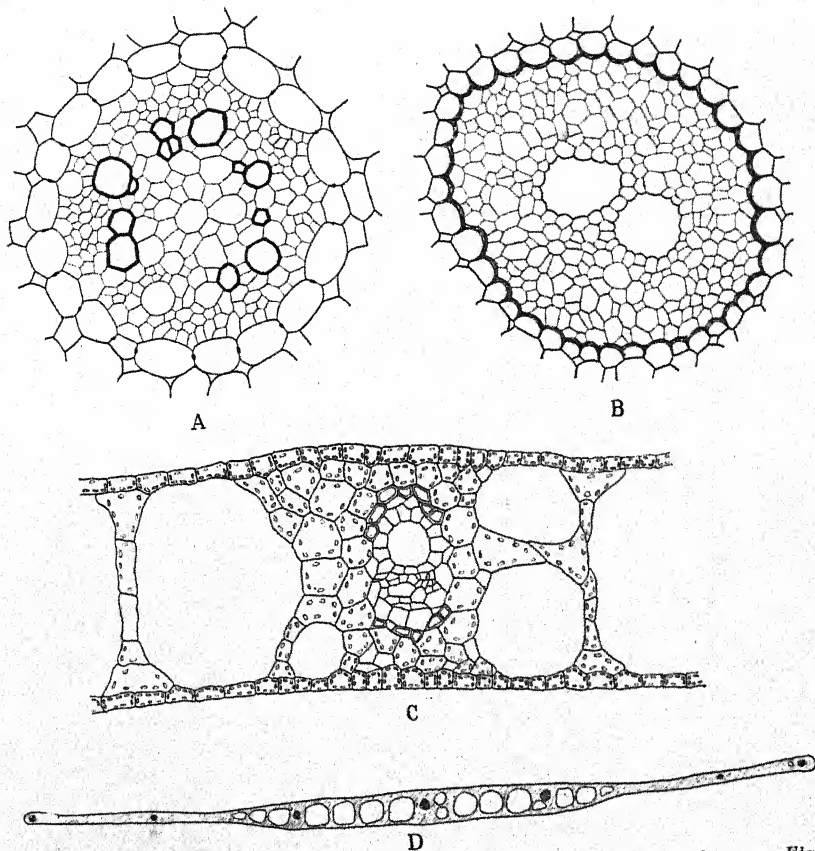


FIG. 139.—Structure of hydrophytes. A, B, cross section of stele of stems, *Elatine Alsinastrum* and *Potamogeton pectinatus*, respectively. A, xylem cylinder greatly reduced; phloem cylinder complete. B, xylem lacking, its position occupied by lacunae; phloem well developed, surrounding the lacunae; inner wall of endodermis much thickened. C, D, cross sections of submerged leaf of *Potamogeton epihydrus*. D, diagram, showing air chambers and bundles. C, detail of central portion of D, showing reduced bundle with the xylem lacking and sclerenchyma reduced; all other cells thin-walled, chloroplasts in the epidermis, stomata lacking. (A, B, after Schenck.)

times known as idioblasts, each with many long-pointed extensions or arms. These have minutely roughened surfaces and are lignified or cutinized. The surface is not readily wet by water; and it is, therefore, thought that these cells prevent the flooding of the entire air-chamber system in case the stem or leaves are broken. The cross-partitions of air

chambers, known as diaphragms, perhaps serve the same purpose. These diaphragms are often perforated with minute openings (Fig. 140, *B*) which supposedly permit the passage of gases but not of water. Air chambers serve also to render the organs in which they occur more buoyant.

Aërenchyma.—Another specialized plant tissue which adds to the buoyancy of certain aquatic plants is that known as *aërenchyma*. This is

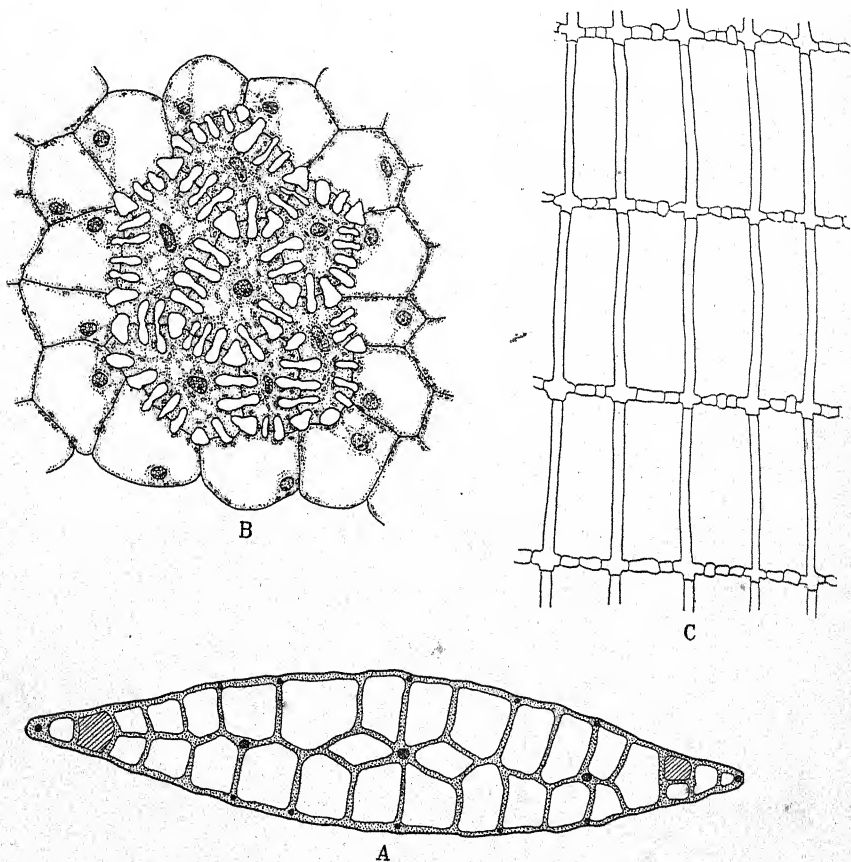


FIG. 140.—Structure of hydrophytes. *A, B, Pontederia cordata*; *A*, cross section of submersed leaf, showing air chambers and reduced vascular bundles (doubly cross-hatched); diaphragms in air chambers singly cross-hatched. *B*, diaphragm in detail showing perforations (unshaded). *C*, aërenchyma in *Decodon*, cross section, showing air spaces formed by elongation of certain cells of each layer of phellem cells.

present for the most part on the stems of plants which grow out over the surface of bodies of water, as, for example, *Decodon* and *Lythrum*, and serves to float the stems which support the leaves of the plant in the air. Structurally, aërenchyma is a very delicate tissue in which thin partitions enclose air spaces extending parallel with the plant axis (Fig. 140, *C*).

This tissue is formed by a phellogen layer, either cortical or epidermal in origin. At regular intervals certain cells of this layer give rise externally to cork cells, greatly elongated in the radial direction. These radially elongated cells form the radial walls of the air chambers. The tangential walls of these chambers are composed of other phellem cells which are not elongated radially and which have become separated from the adjacent tangential rows of cells. In a physiological sense the term "aërenchyma" is applied to any loose aërating tissue. Such tissues may be morphologically a part of the cortex or pith, and hence quite distinct from the typical aërenchyma described above which is formed by phellogen.

Lack of Sclerenchyma.—Submersed plants for the most part lack sclerenchymatous tissues and cells. The support and the protection secured by the presence of these cells are rendered unnecessary because of the buoyant effect of the water and the protection secured by the water against drying and mechanical injury. A certain amount of rigidity is secured by density of cellular structure, thick walls, and in some cases by collenchyma, but submersed plants, especially the leaves and smaller stems, are flaccid and collapse when removed from the water. Sclerenchyma strands occasionally occur, especially along the margins of leaves; here they apparently serve to increase tensile strength.

Reduction of Vascular and Absorbing Tissues.—An aquatic plant is, in reality, submerged in or floating upon a nutrient solution. Adaptations to this environment have, therefore, been in part the reduction or elimination of those structures which, in land plants, function in the absorption of mineral nutrients and water from the soil, and the conduction of these substances throughout the plant. Thus in hydrophytes the root system may be greatly reduced, so that the roots function chiefly as holdfasts or anchors, and a considerable part of the absorption takes place through the leaves. All degrees of reduction of the root system are found. Even where reduction is not extensive, root hairs are usually lacking, and the roots probably do not absorb water to any extent. In the vascular tissues the xylem shows the greatest proportional reduction as this tissue is concerned primarily with the conduction of water, a function which in hydrophytes is not of great importance. In many forms the xylem consists of only a few elements, even in the stele and main vascular bundles (Fig. 139, A). Less commonly in the stele and large bundles, and frequently in the small bundles, xylem elements are lacking. In these cases there is usually a more or less well-defined xylem lacuna to mark the normal position of the xylem (Fig. 139, B, C.) Such spaces resemble typical air chambers. The phloem tissues of aquatics, though reduced in amount as compared with those of mesophytes, are in most cases fairly well developed as compared with the xylem. They resemble the phloem tissue of reduced herbaceous plants generally, in that the

sieve tubes are small as compared with those of the woody plants. The nature of these reduced bundles is illustrated in the leaf of *Potamogeton* (Fig. 139). In aquatics an endodermis is commonly present, though often weakly developed.

Amphibious Plants.—Some situations, such as tide-water marshes and the banks of streams which are subject to flooding, are inundated at rather frequent intervals, so that plants growing there may be exposed alternately to immersion and drying. Plants which are adapted to this type of situation are designated as *amphibious*. The best examples of the type are found among the algae which grow between high and low-tide levels. Some vascular plants, however, particularly grasses and sedges, are of frequent occurrence in such situations and may form most or all of the vegetation in a given area. Plants adapted to this habitat have for the most part the general structure of mesophytes, or of halophytes, if the habitat is a salt marsh. They frequently have, however, special provision which prevents the wetting of the surface and particularly the flooding of the stomata. Such protection is normally afforded by cuticular pegs or by projections of the epidermal cells generally and especially about the stomata (Fig. 136, *D*). As these small structures are not wet by water, a bubble of air is held over the stoma while that portion of the plant is submerged.

Plants of Moist and Shaded Situations.—In the so-called rain forests of the tropics, where conditions of saturated atmosphere and dripping vegetation obtain, a type of environment is produced in which plants show appreciable structural modification. Other factors contributing to rain-forest conditions are reduction of light near the forest floor and lack of winds. The adaptations found as a result of these conditions are, in general, intermediate between those of hydrophytes and mesophytes. ✓ Thus in typical rain-forest undergrowth the epidermis is only slightly cutinized, the stomata are normal and often raised above the leaf surface, and the conducting and supporting tissues are reduced. ✓ The leaves are broad and thin with weakly developed palisade layers, a type commonly known as *shade leaves*. This type of leaf structure is found in many mesophytic plants which are adapted to shaded situations, such as many low-growing woodland plants, for example, *Jeffersonia* (Fig. 141, *C*). The more extreme forms of such habitats lack palisade layers, and may possess an epidermis which contains chloroplasts and becomes a part of the photosynthetic tissue, as in *Cryptogramma* (Fig. 141, *A*), a fern of moist, shaded cliffs.

Hydathodes for the exudation of water are frequently found in plants adapted to growth in a saturated atmosphere. The leaves of the trees forming a large part of the high-growing vegetation in rain forests show in many cases a somewhat xerophytic structure, probably as a response to the conditions of intense tropical light rather than to water relations.

Protection from Animals.—Much has been written about the adaptations which plants show as means of protection against the depredations of animals. The more obvious of these are, of course, the spines, thorns, and stinging hairs which characterize many species. It has been suggested that raphides and other crystals, which are often abundant in aquatic plants and other unprotected soft plants, and in storage organs, may be effective against snails. Gums, tannins, and other substances

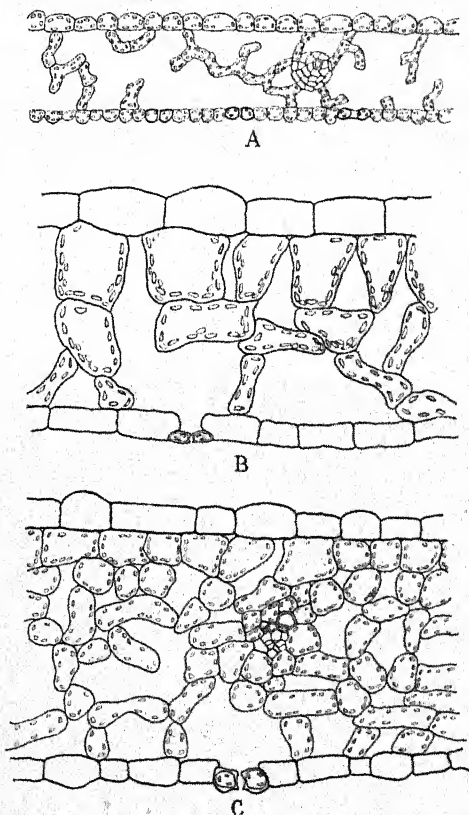


FIG. 141.—Structure of shade leaves. A, *Cryptogramma Stelleri*; B, *Circaea alpina*; C, *Jeffersonia diphylla*. Showing mesophyll loose, and palisade layer weak or lacking, and epidermis weakly cutinized. A, extreme form suggesting hydrophytic condition, with chloroplasts in epidermis.

poisonous or distasteful to animals are common among plants, but the extent to which these are of value as protective structures is uncertain. Many intricate relationships have also been claimed between animals and plants in which plant structure has been modified to serve as shelter or food for certain animals, but the validity of at least some of these is to be questioned. In many cases the modifications are the direct result of stimulation by the animal of the plant tissues through injury or

injection of foreign substances. The varied structure of galls is largely of this nature.

Parasites.—The structural changes discussed earlier in this chapter have been adaptations to environmental conditions dependent in large part upon climate, in which differences of moisture, temperature, light intensity, and similar factors are involved. In the parasitic, saprophytic, and insectivorous vascular plants, however, structural adaptation is not concerned with climate, but with a specialized mode of life in which the plant in question is wholly or in part dependent upon other organisms. Thus, in parasitic vascular plants there are commonly no roots except in the seedling stage before connection with the host is made. Such

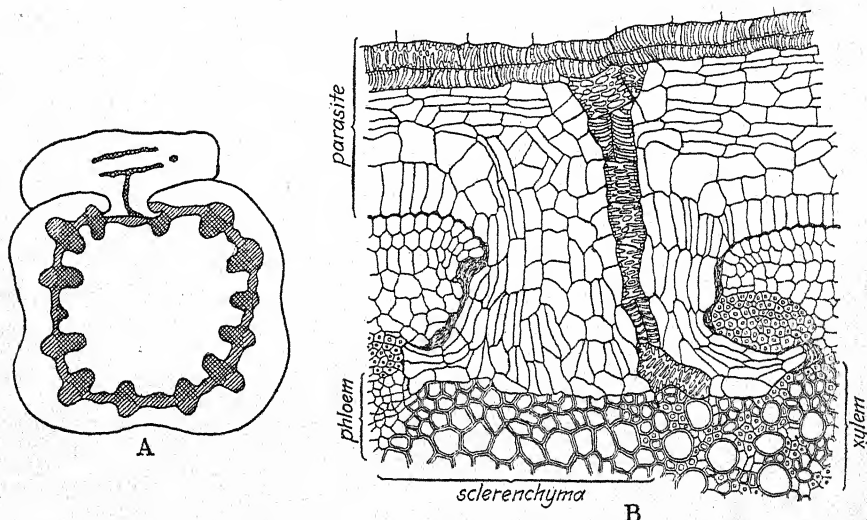


FIG. 142.—Haustorial connection of parasite with host—*Cuscuta* on *Bidens*. A, diagram, showing cross section of stem of host, oblique section of stem of parasite, and longitudinal section of haustorium penetrating host to vascular tissues, which are double cross-hatched, sclerenchyma single cross-hatched. B, detail of haustorium and surrounding tissues. The vascular tissues of parasite connected with those of host.

plants as *Cuscuta* and *Conopholis* are familiar examples of this condition in which, early in the life of the seedling, the parasite establishes direct connection by means of its haustoria with the conducting system of the host. In this connection the xylem and the phloem of the parasite join directly with the same tissues of the host. Thus, the parasite is supplied with water, mineral nutrients, and elaborated plant foods. In establishing such a connection the tissues of the host are dissolved away by enzymes secreted by the parasite at the points of contact where the haustoria of the parasite are formed (Fig. 142). After the connection is once established, new secondary vascular tissues may be formed by the parasite as it develops. These continue the connection with the newly formed tissues of the host.

In the true parasites all tissues concerned with the function of photosynthesis are functionally greatly reduced or entirely wanting, sometimes existing as useless vestigial structures. Thus in such plants as *Cuscuta* and *Arceuthobium*, the leaves are reduced to scales and chlorophyll is wanting throughout the plant. The structures which remain are such as are of value to the plant either in establishing new host connections or in producing seeds in large numbers. In *Cuscuta*, slender naked branches may extend like tentacles in all directions during the vegetative period of growth. These twine about any living plant they touch and haustoria are developed rapidly. Later, great numbers of fruiting branches are produced. Such a plant may form a large number of host connections. Other plants, as, for example, *Conopholis* and *Orobanche*, make only one host connection, but penetrate deeply into the root of the host. In such cases the parasite may form a flowering axis only. Besides these complete parasites which depend wholly upon the host for food and water, there are a considerable number of so-called "half-parasites," which, although connected directly with the vascular tissues of the host, apparently manufacture some part of their own food supply. The mistletoes, *Viscum* and *Phoradendron*, are familiar examples of this type of plant. Here water and mineral nutrients are obtained entirely from the host. Carbohydrates are probably, at least in part, formed by the parasite. The conducting tissues of parasites are commonly much reduced. Sclerenchyma often supplies nearly all the support of the stems.

"**Saprophytes.**"—The term *saprophytes* as commonly applied to vascular plants refers to a group of chlorophyll-lacking forms which have been said to secure their food supply from decaying organic matter, much as do many of the fungi. Many and probably all such plants are associated more or less closely with fungi in their underground parts. The method by which such plants obtain food materials is apparently bound up in some way with the physiological activities of these fungi. The nutrition of saprophytes is thus a very complex matter, and is not well understood. It seems to be clear, however, that such plants are not strictly saprophytes—that they are, to a certain extent, at least, symbiotic with or parasitic upon the lower forms, or are associated in nutrition with them. It seems undesirable at least to call such plants saprophytes until their methods of nutrition are fully understood.

Plants of this type are usually greatly reduced in structure—the leaves are scale-like and the stems are reduced largely to inflorescence axes. Internally, there is also much reduction and simplification of structure. The xylem and the phloem are small in amount and the cells of these tissues often abortive, and sclerenchyma is scarce. The roots may be well developed and abundant in proportion to the aerial parts, as in *Monotropa*, or may be lacking, rhizomes taking their place, as in *Corallorrhiza*. Where roots are present, they are usually of peculiar

structure owing to the association with fungi. Roots of unusual form, together with the fungus hyphae associated with them, form *mycorrhizae*. Two types of such roots are recognized: *ectotrophic*, those in which the mycelium forms a more or less superficial layer or coating about the roots; and *endotrophic*, those in which the hyphae lie within or between the root cells themselves.

In *ectotrophic* forms the fungus hyphae form a tissue-like web about the root, enclosing it like a glove about a finger. The mycelium is closely appressed to the root, and some of the hyphae penetrate between and around the epidermal and subepidermal cells. In some forms there is little penetration between the outer cells, in others the cells of the epidermis and of several outer layers of the cortex may be surrounded by hyphae.

Rootlets invested by fungus hyphae in this way are of unusual structure—they have neither root cap nor root hairs, are of limited growth in length, and are fleshy with their conducting tissues greatly reduced. In *endotrophic* forms also the roots may be enlarged and fleshy, but there is less reduction of vascular tissues. The hyphae are usually restricted to a special part of the cortex where a definite layer of infected cells may occur. In non-green plants the interrelationship of the two plants is obscure.

Mycorrhizae occur on many green plants also; they are known on several genera of forest trees and in many members of the heath family. The relationship of the fungus and vascular plant in green forms is not understood, but it is probable that with forest trees and basidiomycetous fungi, the latter are parasitic upon the former. In some *endotrophic* forms some type of symbiosis may exist.

Insectivorous Plants.—A comparatively small number of vascular plants are specially adapted for the capture and digestion of insects and other small animals. They thus obtain a supply of protein and probably other organic material without synthesis on the part of the plant. The structural adaptations are those which provide for the capture and digestion of the insects and for the absorption of substances obtained from their bodies. In *Sarracenia* and *Nepenthes* the leaves form pitcher-like organs containing water, into which the insects fall after being trapped within the pitcher by various means. Digestive glands secrete enzymes into the water where digestion takes place and from which the proteins are absorbed. The fly traps of *Dionaea* and the tentacles of *Drosera* bring about the same results in a different way. The insects are held by the leaf or its tentacles and digested and absorbed by epidermal glands. The structure of digestive glands is considered in the discussion of secretory tissue in Chapter IV.

Symbionts.—Symbiosis, in which two organisms are associated, each dependent upon the other in some fundamental way, is rare or wanting

among vascular plants. So-called symbiotic relationships have been claimed for the association of the nitrogen-fixing bacteria with the legumes, *Alnus*, *Ceanothus*, and other plants, and for the fungi in mycorrhizal association with the Ericaceae, the orchids, and certain forest trees. In these instances it is apparent that the host plant is benefited, though perhaps indirectly, by the microorganism. The structural modifications of the "nodules," which are modified rootlets, however, are more of the nature of galls or abnormalities caused by parasites, and therefore belong rather in the field of pathological histology than in the present treatment.

In any discussion of the adaptation of plants to their environments, the terminology used for the sake of convenience is likely to give the impression that the environment in some way has caused the plant to produce the adaptation or that the plant in some way consciously or purposely has done something to meet the situation. This, of course, is not the fact, as the effect of environment has doubtless been for the most part, merely to eliminate forms which are unable to withstand the existing conditions. With some structures environment may have been a direct cause of adaptation, as, for example, the probable production of heavily lignified tissues under conditions of intense light. The production of quantities of lignified tissue under such circumstances might possibly be the result of the increased photosynthesis or other chemical change due to the increased light. Just how the changes of structure are initiated is not known. The vast period of time over which the selective action of environment has been operative, and the possible value of slight variations must always be borne in mind.

The above discussion is only a very brief statement of some structural adaptations of plants to their environment. In nature the details of such adaptation are almost infinite in number and variety. All may, however, be interpreted on a basis of comparison with the structural features of mesophytic plants.

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CHAPTER XV

A SKETCH OF THE HISTORY OF PLANT ANATOMY

Among the various fields of present-day botany, anatomy is often considered to be largely of recent development. And such it is in certain aspects, especially those of the understanding of the morphology and phylogeny of both gross and minute features of structure, and those of knowledge of the detailed structure of complex tissues. Yet anatomy had its beginnings—beginnings as extensive and as important as those of taxonomy and morphology—in the studies of the Greeks in the last few centuries before Christ; and its foundations were laid in the seventeenth century, when it became more firmly established than taxonomy, morphology, or physiology.

The advanced position of anatomy in botanical science in the seventeenth century was, however, only temporarily maintained; during the following period of nearly two centuries progress was slow and vacillating. Meanwhile, taxonomy progressed through the important Linnaean period, and physiology through the times of Hales, Priestley, and others, to an equally important foundation. In anatomy, substantial progress began again in the middle of the nineteenth century, and at this time and during the decades immediately following, it perhaps may be said to have attained its maximum rate of development. Since this period there has been slow and steady progress, with somewhat more rapid development along certain lines in the past twenty-five or thirty-five years.

Throughout its progress, development in anatomy has been to a large extent dependent upon the stimulus of interest in some allied field. When paleobotany turned to interpretations based upon anatomy, the great impetus given to its own progress and to interest in phylogeny extended also to anatomy and vitally influenced the progress of this field of study. Advance in anatomy—after the first steps were taken in the sixteenth century and again in the early nineteenth century—has been, throughout, to a very large extent due to interest in comparative morphology. Only for brief periods has descriptive anatomy, as such, prevailed, and only rarely has descriptive or physiological anatomy contributed substantially to increased knowledge of the field. The fact that comparative morphology has dominated advance in anatomy has been of the greatest value in the laying of a solid foundation; study in this field has made clear the fact that only on such a basis can the most

satisfactory progress be made. The most recent advances in anatomy have also been connected with the pursuit of phylogenetic studies. Anatomy is to an increasingly greater extent playing a part in the establishment of a natural system of classification—the goal toward which the efforts of morphological and taxonomic study are directed.

Anatomical study began in England, and since the days of Nehemiah Grew has continued almost without interruption in that country. During a large part of the nineteenth century the leading workers were in Germany and France; at the end of the century, however, the center of anatomical research passed back to England. The maintenance of interest in anatomy in England is doubtless due in large measure to the fact that early important studies were made there; to the development of paleobotany by the anatomical study of the wonderfully preserved flora of the English coal measures; and to the stimulus given to the study of the comparative anatomy of living forms by the study of the structure of ancient plants. It is, therefore, natural that English anatomists should direct their attention to comparative morphology and phylogeny. In Germany, the latter viewpoint has played an unimportant part; the numerous, important, and extensive studies made in that country have presented detailed structure with great accuracy, but are, as a whole, largely without correlation as to morphological or taxonomic meaning. Physiological plant anatomy has come almost wholly from Germany. In France, there has been a tendency toward broad morphological studies of a comparative nature, and these were numerous in the last quarter of the nineteenth century. In the United States anatomy has not at any time been a "popular field" of study; and only in the past thirty-five years has important research in this field been carried on here. Valuable results have come, however, from the restricted number of studies thus far made, throughout which the influence of the English viewpoint is dominant.

The Beginnings of Anatomy.—The interest of mankind in plants in a way that can be called truly scientific began, so far as we know, with the Greeks in the last centuries before the Christian era. Rudiments of the science of botany exist in the writings of the ancient Greeks of this time, but only in the books of Theophrastus of Eresus (about 369–262 B. C.) are distinctly botanical treatises found. Aristotle, the tutor and friend of Theophrastus, is known to have written extensively about plants, but these writings have been lost. The discussions of Theophrastus are philosophical in nature. His essays on structure deal with the kinds of organs, the relation of organ to organ, and of kind of organ to kind of organ. He distinguished in a tree, root, stem, branch, leaf, flower, fruit, and maintains that this is a normal sequence; he even recognizes roots, as such, when they are aerial. Thus he established the beginnings of descriptive morphology. These morphological studies he extended

to gross internal features, to the anatomical structure of stems, roots, and leaves. He says: "Plants are made up of bark (*phloios*), wood (*zylon*), and pith (*metra*), when pith is present." Thus, two of the best-known and most-used anatomical terms, phloem and xylem, go back, in approximately their present form, to the very beginnings of anatomy; they are, indeed, classic terms. By the use of these distinctions Theophrastus describes in a rough way the gross differences in the stems of dicotyledons and monocotyledons, and even discusses the nature of annual rings.

Theophrastus describes the stem in more detail, as a fabric of veins, nerves, and flesh, not implying by these terms, however, homology with animal tissues. Veins and nerves are essentially one and the same, the nerves being the minute fiber-like parts, the veins the larger strands, apparently the vascular bundles. Veins and nerves are characterized by the fact that they can be split, but not otherwise readily separated; whereas flesh can be readily divided in all planes "like a lump of earth." Here is the beginning of the old anatomical classification of tissues—one to which at present occasional reference can still be found—as prosenchyma and parenchyma. Having distinguished the elements of the plant body, Theophrastus was able to state that wood is composed of nerves and moisture; pith, of flesh and sap; bark, of nerves, flesh, and sap. Here was made a real beginning of an acquaintance with the structure of plants. Thus did Theophrastus lay foundations in morphology and anatomy. At the same time he made important beginnings in classification, especially in nomenclature; many of our present-day generic names were first used by Theophrastus. For these reasons this Greek student of the third century before Christ has been called the father of botanical science. This may be said of him with especial significance as regards anatomy.

After the meager and crude, but still fundamental, contributions of Theophrastus to the science of botany, the interest of the Greeks in pure botany rapidly declined; and though botanical study was continued sporadically for a few centuries by them and by the Romans, it took the form of the application of botanical knowledge to medicine and agriculture. With the rise of the Christian doctrines, which stilled by their authoritative statements all inquiry into the origin and nature of living things, began the "Dark Ages" of biological science. For botany this period began to lighten only in the early part of the sixteenth century with the studies of the herbalists, and with the advances in classification made at the end of this and during the early part of the succeeding century. Throughout this period, which was one of progress in taxonomy alone, plant description was based on external morphology, since means of magnification were then unknown. Only by Valerius Cordus (1515-1544) and Andrea Caesalpino (1519-1603) were investigations of the internal structure of plants made. The former added brief descrip-

tions of stem and petiole sections to his taxonomic descriptions, and the Italian botanist in his philosophical speculations made suggestions as to the anatomy of the plant which he gained in his search for its soul. Doubtless, Caesalpino's search was in large part theoretical, as he played a prominent part in starting the wave of interest in "idealistic" morphology which swept the field of morphological study during the next two centuries, and culminated in the philosophical morphology of Goethe and his followers. Though all Caesalpino wrote was obscured by Aristotelian philosophy, he appears to have made many good observations, and to have restarted botany on a basis of more exact terminology. Caesalpino postulated the presence of canals for conduction, and observed that many roots lacked pith. However, in the sixteenth century, nothing of moment was accomplished to break the long blank interval of nearly nineteen hundred years from the time of Theophrastus to the sudden awakening of anatomy in 1671.

The Discovery of the Cell.—In the middle of the seventeenth century a new field of botanical research was abruptly established by the use of lenses to determine details of internal structure. Curiosity as to the minute structure of plants led quickly to the rise of anatomy. One of the first of the investigators who examined all sorts of things with the "new toy," the magnifying lens, "to see what they were like" was the Englishman, Robert Hooke (1635-1703). Hooke, more or less incidentally—he was a mathematician and an architect, and not in any way actually interested in plants—found in connection with his examination of various things under the lens that plant tissues are made up of units which he termed "cells." He found that cork and charcoal, as well as other tissues, are "perforated and porous, much like a honeycomb." To the cavities of such honeycomb-like structures Hooke applied the term *cell*. The walls were *interstitia*, and not parts of the cell in his interpretation. Not until the beginning of the nineteenth century was it recognized that a part of the interstitial substance is definitely related to each cavity. Hooke published his discovery of plant cells in 1665 in his *Micrographica*, together with descriptions of many other structures seen through the lens. Thus it was a microscopist—for Hooke cannot be considered a botanist—who made a discovery of the greatest importance to the science of botany.

The Founders of Plant Anatomy.—The immediate value of Hooke's researches, however, was the stimulus they imparted to studies of plant structure. These studies bore fruit in the foundation works of Marcello Malpighi (1628-1694) and Nehemiah Grew (1641-1712), which appeared in the years immediately following. The suggestions of Hooke led to the systematic study of plant tissues by Grew, an English physician, and by Malpighi, an Italian physician and university professor. These men, working independently, each knowing nothing of the studies of the

other, presented at the same time monographs on the structure of plants which stood for a century as the standard works in this field. Both men approached the study of plants from the standpoint of medicine, hoping to find in plants structural conditions comparable with those in animals. Grew studied plant structure for several years before presenting "The Anatomy of Vegetables Begun," which was published by the Royal

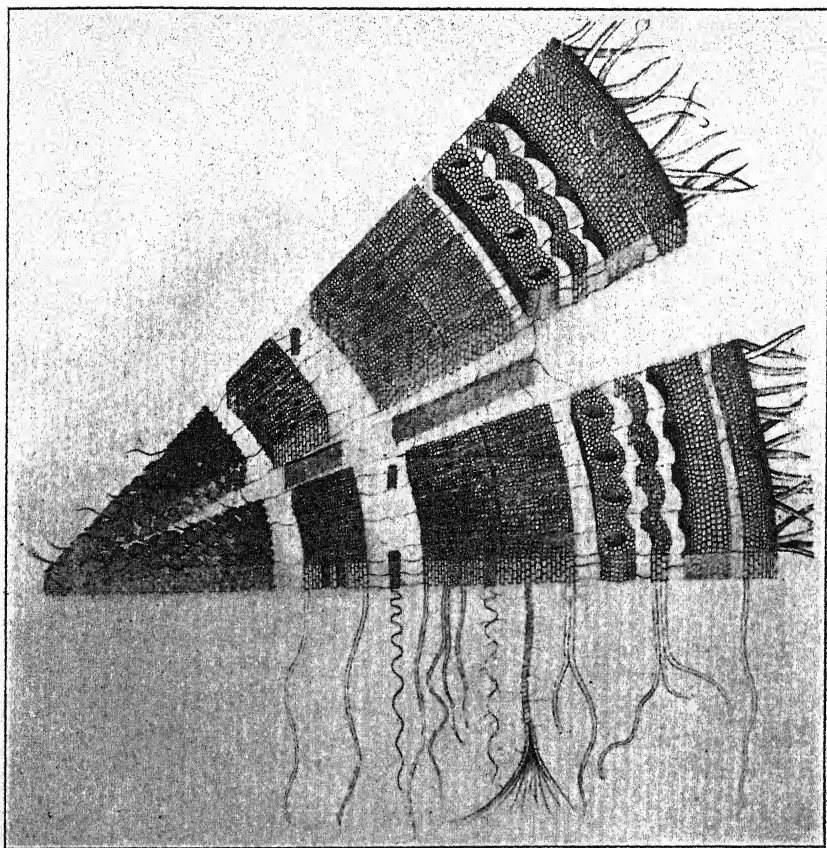


FIG. 143.—"Sumach Branch, cut transversely . . . with several breaks to shew ye Contexture both of ye Perpendicular & Horizontal Fibers." (*The Anatomy of Plants*, Nehemiah Grew, 1682.)

Society in 1672, and presented in print at the very time when the Society received Malpighi's manuscript dealing with the same subject. There seems to be no question but that the work of Grew deserves priority, though the papers of both men were received by the Society at the same time; nor is there any question but that the work of each was wholly independent of that of the other. In their later studies, however, each

owed much of suggestion and information to the other. Grew's first publication was morphological, largely, rather than anatomical; it was followed by three others, more strictly anatomical in nature, the final treatise, published in 1682, being "The Anatomy of Plants, With an Idea of Philosophical History of Plants, and Several Other Lectures, Read before the Royal Society." In these four papers Grew discusses the grosser structure of plants, contrasting the vascular skeleton with that of animals, and describes the finer structure in much detail. This seems to have been done with infinite care and great skill. His detail does not to any great extent reach to the description of the cell itself, but deals largely with the manner in which tissues are built up of cells. He thought of the tissue of plants as a complex web of fine threads (Fig. 143):

The most unfeigned and proper assemblance we can at present make of the whole *Body* of a *Plant*, is, To a piece of fine *Bone-Lace*, when the women are working it upon the *Cushion*; For the *Pith*, *Insertions* [rays], and *Parenchyma* of the *Barque*, are all extream Fine and Perfect Lace-work; the *Fibers* of the *Pith* running *Horizontally*, as do the *Threds* in a Piece of *Lace*; and bounding the several *Bladders* of the *Pith* and *Barque*, as the *Threds* do the several *Holes* of the *Lace*; and making up the *Insertions* without *Bladders*, or with very small ones, as the same *Threds* likewise do the *Close Parts* of the *Lace*, which they call the *Cloth-Work*. And lastly, both the *Lignous* and *Aer-vessels*, stand all *Perpendicular*, and so cross to the *Horizontal Fibers* of all the said *Parenchymatous Parts*; even as in a Piece of *Lace* upon the *Cushion*, the *Pins* do to the *Threds*. The *Pins* being also conceived to be *Tubular*, and prolonged to any length; and the same *Lace-work* to be wrought many *Thousands* of times over and over again, to any thickness or hight, according to the hight of a *Plant*; and the *general composure*, not only of a *Branch*, but of all other *Parts* from the *Seed* to the *Seed*.

Thus Grew recognized, in a way, vertical and horizontal systems, and the constancy of these conditions throughout the plant.

Grew presents a classification of plant tissues, which in its crude separation of prosenchyma from parenchyma is essentially the same as the classification of Theophrastus. In his own words:

All the *Parts* of a *Vegetable*, the *Root*, *Trunk*, *Branch*, *Leaf*, *Flower*, *Fruit*, and *Seed*, are still made up of *Two* substantially different *Bodies* . . . All properly *Woody Parts*, *Strings* and *Fibers* are *One Body*: All simple *Barques*, *Piths*, *Parenchymas* and *Pulps* . . . all but *One Body*, the several *Parts* of a *Vegetable* all differing from each other, only by the various *Proportions* and *Mixtures*, and variated *Pores* and *Structure* of these *Two Bodies*.

It is apparent that Grew understood the method of secondary growth. This takes place, he says,

. . . betwixt the *Wood* and *Barque* . . . every year the *Barque* of a *Tree* is divided into *Two Parts*, and distributed two *contrary* ways. The outer *Part* falleth off

toward the *Skin*; and at length becomes the *Skin* it self . . . The inmost portion of the *Barque* is annually distributed and added to the *Wood*; . . . So that a *Ring of Lymphaeducts* in the *Barque* this year, will be a *Ring of Wood* the next; and so another *Ring of Lymphaeducts* and of *Wood*, successively, from year to year.

An important structural condition seen by Grew is the fact that the xylem in the roots is radially arranged, and that the vascular tissue of roots forms a solid core and that of stems a hollow cylinder. In plants, Grew looked for vessels like those of animals, and found them in spiral vessels—already discovered by Malpighi—which he describes with precision. However he knew only the “fine narrow Ribband, woun’d spirally, and Edg to Edg;” the primary wall was not seen. He could see and understand parenchyma better than other tissues. Parenchyma to him was “an infinite Mass of little Cells or Bladders. The sides of none of them, are Visibly bounded within itself. So that the *Parenchyma* of the *Barque*, is much the same thing, as to its conformation, which the Froth of *Beer* or *Eggs* is, as a fluid . . .”

The terms “parenchyma” and “vessel” thus go back to Grew in much the sense of present-day use. Other terms, such as “cuticle” and “cortex,” apparently first used by him, have today different values.

There are evidences in a personally annotated copy of “The Anatomy” that Grew after the publication of his papers also studied the ontogeny of tissues; in his notes he observes: “Air-vessels of Parenchyma, transformed, as Caterpillars to Flies.”¹

Grew’s work was colored by the philosophical tendencies of the time, but to a surprisingly small extent. In his mild manner, he protests against the growing idealistic conception that it is “according to the *idea* of the philosophers that things are so and so, no matter what the actual condition is.”

“Grew believed that the ‘Outward Elegancies of *Plants*’ might be for the purpose of giving delight to the human race, but he was the first to point out that as the ‘Inward Ones, which, generally, are as Precise and Various as the Outward,’ are so seldom seen, their purpose can hardly be for this, but must be for the benefit of the plants themselves, ‘That the *Corn* might grow, so; and the *Flower*, so, whether or no Men had a mind, leisure, or ability to understand *how*.’”²

This was a strong statement at a time when it was believed that the purpose of the entire organic world was but to serve mankind, when it was held by some that even the fossils in the rocks were divinely created ornamentations of the interior of the earth for the pleasure of man whenever he might happen upon them. Grew was, indeed, a man before his time, and well deserves the title of “founder of plant anatomy.”

¹ “Makers of British Botany,” p. 52.

² “Makers of British Botany,” p. 64.

Malpighi's work covered much the same ground as that of Grew, and his conceptions were much like those of his fellow worker, but were even less affected by philosophical considerations. In his generalizations he was, however, less acute and less thorough than the English anatomist. Like Grew, Malpighi believed wood to be derived from the inner bark by transformation, an opinion very closely correct, as can readily be understood. Credit should be given Malpighi for the discovery of spiral vessels—a discovery which Grew later expanded—and for the discovery of stomata. Like Grew, he speaks freely of tissues as made up of bladders, utricles, and fibers, but he did not understand these to be cells as they are thought of today. He saw tyloses and illustrated them, but quite naturally, did not distinguish them from other "bladders." Many of the terms used by Grew were taken up by Malpighi. The latter, himself, established few terms; his Latin term *liber* for the fibrous elements disposed in sheets in the inner "cortex" persisted for a very long time, only gradually to be replaced by the Anglo-Saxon *bast*.

Both Grew and Malpighi related their anatomical discoveries to function, and carried physiological investigations to a stage in many ways comparable with that reached in their studies of structure. On this account they have been called physiological anatomists. Grew dealt especially with function as related to structure in his investigations of the movements of sap. Both of these investigators also made morphological studies of flowers, leaves, and roots.

The Eighteenth Century.—After the death of Grew, interest in plant anatomy waned in England, but rose slowly on the continent of Europe, where increasing numbers of students took up this field, attracted doubtless by the opportunities presented by the constantly improved microscope. Through the eighteenth century the errors and misconceptions of the two anatomists of the preceding century were gradually removed, but only too often were replaced by others equally bad or even worse. The prevalent idea that all vessels were spiral was banished by the Dutch student, Antony van Leeuwenhoek (1632-1723), who first described pitted vessels. The study of the growing layer of the "inner Rind," begun by Grew and Malpighi, was continued by the French arboriculturist, Du Hamel (1700-1781), who gave the term *cambium* to "a gelatinous generative zone in the inner cortex." In Germany, Caspar Friedrich Wolff (1733-1794) studied plants persistently under the influence of the idealistic morphology which was then at its height. Wolff's theory that a tissue is a homogeneous matrix "filled with bubbles, as is rising dough," stimulated research in the nature of tissue, and this research became productive of most important results in the early part of the next century. The eighteenth century was a period of slight progress in all fields of botany with the exception of taxonomy;

descriptive morphology made but little advance, and "internal morphology," anatomy, but little more. During the entire century no advance of importance was made in anatomy, and no work replaced that of Malpighi and Grew until well into the nineteenth century.

The Nineteenth Century.—In France, anatomy was founded by Charles Francois Mirbel (1776-1854), who elaborated Wolff's theory, stating that new cells appear in a homogeneous matrix as cavities which have openings into one another for the passage of sap. Mirbel was vigorously opposed in his theory of tissue structure and of cell origin by Kurt Sprengel (1766-1833); and, though the controversy in which they became involved produced little result in the way of new or more accurate information as to the nature and origin of the cavities known as cells, it brought anatomy again into prominence. Sprengel agreed with Mirbel that cells opened into one another, but stated that new cells arise within the contents of old cells as small vesicles which become enlarged by absorption of water. (These "vesicles" were probably starch grains.) In this theory Sprengel was supported for many years by Ludolph Christian Treviranus (1779-1864). Treviranus, while studying growing tissues, made the important discovery that vessels were formed from series of cells by the disappearance of cross-walls. (Grew had not understood the transformation, and had not published his observations on vessel formation.) Treviranus also first saw the development of the spiral band in protoxylem cells.

The study of cell ontogeny thus initiated by Treviranus was continued by Johann Jakob Bernhardt (1774-1850), who was a more accurate observer and more original in his methods of study. He discovered annular elements, and recognized that in them and in spiral cells the thickened rings and bands were tied together by a primary wall. He noted that this type of cell does not occur in secondary wood. He stated that a spiral vessel never changes its nature as claimed by the metamorphosists, who—at this time at the height of the influence of fanciful conceptions—extended their philosophy to cover all parts of the plant.

The discussions of Mirbel, Sprengel, and others concerning the origin of these cavities naturally led to further study of the matrix in which they lay, the "interstitia" of Hooke. In the study of these, Johann Jakob Paul Moldenhawer (1766-1827) introduced the new method of maceration, and, by means of this, at once demonstrated that each "cell" had a wall of its own, and that the cavities were, therefore, separated by two walls, not one. Thus was banished the view of Wolff, Mirbel, and others that the cells were like bubbles in a structureless matrix. Moldenhawer called attention to the union of fibers, vessels, and parenchyma in definite strands and gave to such masses the term *fibrovascular bundle*, a term which is only now being supplanted by the better form, *vascular bundle*.

It is evident that Moldenhawer saw clearly the compound nature of the bundle, and this conception enabled him to look upon the stem of a dicotyledon as made up of vascular bundles which gradually fuse to form a woody cylinder, another morphologically incorrect idea which has persisted to the present day.

The discovery of the individuality of the cell wall stimulated the study of this structure, and a long controversy arose as to its origin and nature. In the study of the cell, the cell cavity yielded the position of importance to the cell wall, which now became "the cell," the contents of the cavity being thought of merely as "cell contents" or "nutrient sap." Interest in the latter was thus, for the time being, subordinate, though it came to the front briefly in 1831 through the "discovery"



FIG. 144.—Hugo von Mohl (1805-1872).

of the nucleus by Robert Brown (1773-1858). The nucleus, however, had been noted by others before, though no suggestions as to its probable importance had been made.

The controversy over the origin and nature of the cell wall naturally involved the origin of cells themselves, and the first suggestions of cell division, as distinct from free cell formation, seem to have been made by Franz Julius Ferdinand Meyen (1804-1840). Meyen, however, did not carry his investigations of cell division very far. His interest lay not in studying structure, but in writing about it. Further, his observations were, unfortunately, inaccurate. He stated

that there were only three kinds of "tissue organs"—cells, spiral tubes, and sap vessels; in this statement he neglected the discoveries of Treviranus that vessels consist of fused cells, and went back for the basis of most of his statements to the opinions of older writers.

The attention given to the cell wall was, however, soon replaced by the rapidly increasing interest in the "cell contents." To students of cellular structure it became increasingly evident that the most important part of the cell was this "contents," from which attention had been temporarily turned away. This opinion was first strongly expressed by Hugo von Mohl (1805-1872—Fig. 144), who emphasized the fact that the contents were "living," and named the vacuolated body the *primordial utricle*. Von Mohl, in his earlier work, was prejudiced by the views of

the older anatomists, and doubtless drew the term "utricule" from them. The great structural and functional importance of the "primordial utricule" soon became apparent, and, though the term was an unfortunate one in several ways, it persisted for a long time. Von Mohl stated that the utricule was made up of *protoplasm*, a term which was already in use by zoölogists for the contents of animal eggs. With the recognition of the fundamental nature of the protoplast, thus initiated by von Mohl, the use of the term "cell" became more or less fixed in the sense of protoplast; and this interpretation of the term—the wall being merely a limiting or protecting secretion of the cell, and not a part of the living cell—has persisted largely to the present day. Occasional efforts have been made to demonstrate that the wall is definitely a part of the living cell, that is, that it is composed, at least in part, of living material. In this question of the possibly partly protoplasmic nature of the wall of living cells there seems to be at present renewed interest. An answer to the question would definitely end the vacillation in the meaning of the term "cell" between lumen, wall, protoplast, and protoplast plus wall, which began with Hooke and continues today.

The Cell Theory.—The great stimulus given to the study of cell contents by the discovery of the similarity of "protoplasm" in animal and plant cells, added to the ever-increasing information as to the omnipresence of cells, soon resulted in the beginning of a theory of the structure of organic bodies. This foundation was laid by Matthias Jacob Schleiden (1804–1881) and Theodor Schwann (1810–1882), who worked on plant and animal tissues, respectively. Independently, they became acquainted with the structure of cells.

When the information each had acquired was brought together—in personal discussion and laboratory study, so the story goes—they became of the opinion that cells are fundamentally alike throughout the plant and animal worlds. As a result of this decision, each produced in 1838 a treatise on the subject, that of Schwann, which he himself termed "The Cell Theory," being the more comprehensive. Schwann says:

The elementary parts of all tissues are formed of cells in an analogous, though very diversified, manner, so that it may be asserted *that there is one universal principle of development for the elementary parts of organisms, however different, and that this principle is the formation of cells . . .* The development of the proposition that there exists one general principle for the formation of all organic productions, and that this principle is the formation of cells, as well as the conclusions which may be drawn from this proposition, may be comprised under the term *Cell Theory*.

Both Schleiden and Schwann were thus concerned in the proposal of the theory that the body of organisms is composed of cells and cell products. The tremendous importance of this to the science of biology was at once recognized by students in both fields. In botany, interest was

turned abruptly from the study of vascular anatomy and the ontogeny of tissues to the new field. Immediately, controversies arose over the method of cell formation, the rôle of the nucleus, the nature of protoplasm, and over other similar problems which are now looked upon as cytological, and with which, therefore, the present sketch need not deal.

In the years just preceding the presentation of the cell theory, the first studies of the structure of fossil plants—by Cotta in 1832 and Witham in 1833—began to stimulate the development of anatomy. Thus, very early began the contributions of paleobotany to anatomy, contributions which have been of the greatest importance in the development of the subject. Indeed, woody plants soon became better known anatomically in a fossil than in a living state. The influence of the study

of the internal structure of fossil plants upon anatomy has continued to the present; it was doubtless greatest in the last third of the century when paleobotany and phylogeny advanced rapidly. The attempts to establish the identity and the relationships of fossil plants led naturally to an emphasis on comparative morphology and phylogeny. And, since external morphological features were often lacking, or considered to be of little value, attention turned to internal structure. Anatomy was forced to progress in order that it might fulfil the demands made upon it for explanation of the structure of fossil plants. Compared with paleobotany, taxonomy and physiology have had



FIG. 145.—Carl von Nägeli (1817–1891).

little effect upon the progress of anatomy.

The period during which the cell theory appeared, the second quarter of the nineteenth century, was one of great activity in anatomical research. Among other fields of botany, only in morphology and taxonomy can it be said that comparable progress was made. The great advances made were due largely to the work of von Mohl and Carl Wilhelm von Nägeli (1817–1891—Fig. 145). Both of these men were turned from the immediate fields of their research—histological studies—to enter the all-absorbing discussion of the cell theory, and contributed to its elaboration in important ways; both later returned, however, to the study of tissues and cell structure. Von Mohl was an unprejudiced investigator, thorough and accurate in the details of his work, and unhampered by philosophical considerations or by the physiological conceptions

of the day. His first work of importance concerned cell ontogeny, in which he demonstrated the progressive thickening of the wall and the relation of secondary to primary layers, disposing finally of the old "transformation" views, such as, that the spiral vessel gave rise by metamorphosis to all other types. Von Mohl's painstaking and accurate observations put an end definitely to the two-century-long, fanciful philosophy of metamorphosis, and of idealistic morphology. In connection with wall development, von Mohl learned that pits are thin places in the wall and not pores or projections; also that the "intercellular substance" was the primary wall. Out of his studies of cell-wall development grew his theory of wall thickening by apposition.

Von Mohl's contributions to anatomy are numerous and most varied. He determined the nature and method of formation of vessels. He described the structure of the epidermis and demonstrated the nature of the cuticle; also the nature of lenticels and of cork, and the consequent formation of "bark" with its constant loss and renewal. Some of these tissue descriptions had, however, been outlined by Grew. Von Mohl first traced the course of bundles, both in monocotyledons and in dicotyledons, and confirmed their complex nature; in the ontogeny of the stem he showed that the first bundles of the stem were bundles connecting with the leaves.

In von Mohl's work we have for the first time accuracy of observation and of statement; with it opens a new epoch in plant anatomy. So excellent was von Mohl's work that much of it stands unquestioned today.

A classification of tissues was made by Franz Unger (1800-1870), but this was wholly empirical and had no morphological basis whatever. As a classification it was not followed to any extent, chiefly because a much better one soon appeared in the work of Nägeli. Unger's classification was, however, the best that had been proposed up to that time. Unger took part in the discussions of the cell theory, entered the controversy as to the method of cell origin, and contributed to the ontogenetic studies so popular at that time. However, it is chiefly Unger's textbook of anatomy and physiology, one of the first good texts in these fields, which brings this most versatile botanist into the field of anatomy, for Unger's major endeavors lay in pathology and paleobotany.

The study of vascular bundles led Hermann Schacht (1824-1864) to claim that the separate bundles of an axis arose by the "branching" of solid cylinders. At the time this was considered absurd, and distinctly a retrograde step in anatomy; and as such it has continued to be looked upon until very recently. However, Schacht was not, of course, thinking of the phylogenetic development of bundles and steles.

Theodor Hartig (1805-1880), a keen observer, who worked chiefly on wood and phloem, discovered the sieve tube and claimed that it was

perforated. Von Mohl disputed the fact of its perforation, but Nägeli later substantiated Hartig's claim.

Nägeli's attention, like von Mohl's, was largely centered on ontogeny. He studied apical meristems particularly, and traced the segments of the meristem from apical cells and apical meristems to mature tissues and organs. From this he passed naturally to the study of the development of vascular bundles from procambial strands. He classified tissues as *generative* and *permanent*, dividing each of these into parenchymatous and prosenchymatous types. To prosenchymatous generative tissues he applied the term "cambium," a term which had been used earlier by Du Hamel, but in the very loose sense of a structureless matrix in which cells arose. Nägeli distinguished between primary and secondary meristems, and introduced the theory of wall thickening by intussusception. He studied sieve tubes in secondary phloem and put forward essentially the theory of their function that is chiefly held today—that they serve for conduction of the less diffusible plastic materials. In the study of vascular bundles he distinguished between cauline, common, and foliar strands. To the parts of the bundle he applied the terms "xylem" and "phloem," not understanding, however, a difference of function in the two parts. Nägeli is commonly looked upon as the originator of the terms "xylem" and "phloem," and for their present form he does appear to be responsible. However, Theophrastus had already used them in slightly different form, though in much the same sense.

Though von Mohl avoided generalizations to a fault, Nägeli made most comprehensive studies, and drew definitely clear conclusions from his numerous data. The clarity and usefulness of von Mohl's and Nägeli's classifications and conclusions are due to the morphological basis which they adopted for their studies. Through this, many obscure points in the older anatomy were readily cleared up. With the work of von Mohl and Nägeli, anatomy begins to resemble in its terms and in its methods the anatomy of today. It may well be said that the modern epoch was ushered in by these two men.

Grew and Malpighi laid a substantial foundation for the science of plant anatomy; Nägeli and von Mohl built its superstructure. More recent workers have determined the principles of construction and elaborated the superstructure, adding details, but have modified the framework only in minor ways.

The Modern Period.—Following the establishment of the cell theory, and of a substantial understanding of cell division, of meristem development, and of fundamental vascular bundle structure, attention centered for some time on the meristems, especially on the cambium, and upon the origin and structure of secondary tissues, particularly xylem and periderm. The acquisition of correct information in these fields was largely due to the efforts of Carl Sanio (1832–1891), a Prussian school teacher.

Sanio established the place and the method of origin of the cambium, and studied the activities of this meristem as related to the formation of annual rings. He worked extensively also on the structure of wood, accurately describing gymnosperm wood in remarkable detail considering the microscopes available to him. Bars of Sanio and trabeculae were first described by him, and bordered pits, the general nature of which had already been learned by Schacht, were also described in accurate detail. He extended his studies of the ontogeny of the secondary tissues to the periderm, the development of which he followed through. Sanio is perhaps best known for his studies in the comparative anatomy of gymnosperm and dicotyledon stems, in which studies he placed emphasis on the elements of the wood, their structure and distribution. The details of wood structure thus first accurately portrayed, together with his discovery of the procambial "thickening ring," constitute probably his most important contributions. Though the nature of secondary growth and of the annual ring had long been known in a general way, the ontogenetic beginnings of such growth were wholly obscure. These Sanio presented definitely, demonstrating place and method of origin of primary bundles and the relation of the cambium to these strands.

Sanio was one of the most prominent anatomists of his time, in method and viewpoint resembling Nägeli. With Nägeli and von Mohl, he should be associated as one of the founders of modern anatomy, and in this respect he is deserving of more credit than is commonly given him. His work surpassed that of Nägeli in accuracy and, in some respects, in importance, as did Nägeli's that of von Mohl.

Sanio's study of meristem development led Johannes von Hanstein (1822-1880), who had been working along lines similar to those followed by Sanio and Nägeli, into the same field. Hanstein showed the origin of Sanio's "thickening ring," by distinguishing in root and stem tips three definite histogenic layers which give rise to epidermis, cortex, and vascular cylinder. To these "histogens" he gave the names *dermatogen*, *periblem*, and *plerome*, respectively. Under the sway of the strong morphological tendencies of the time, Hanstein ascribed to these three layers definite morphological value, and believed them constant in value and in occurrence. Over this opinion controversy quickly arose. Though De Bary soon showed that the theory could not be applied universally and that the histogens lacked morphological value, the controversy continued until the end of the century, and even today Hanstein's histogens are commonly believed to be of characteristic and constant occurrence.

Heinrich Anton De Bary (1831-1888), a student primarily of the fungi, brought together in 1877 the knowledge of anatomy up to that date, publishing at that time his extensive "Comparative Anatomy of the

Phanerogams and Ferns." This book presents the enormous amount of information available at that time, arranged in a way which can only be said to be De Bary's own, and established a reasonable and workable terminology. The content of the book is arranged with little logical sequence; the treatment gives little idea of morphological and still less of physiological distinction; and from it can hardly be readily obtained a comprehensive understanding of the general structure of a plant. Yet so critically have the facts been judged and so accurately and completely have they been presented that De Bary's textbook is of the greatest value and has been the most generally useful and usable reference book in plant anatomy during the nearly fifty years since its appearance. Today it still stands an excellent reference text, the most valuable of all such books.

Physiological Anatomy.—As it became increasingly evident that Hanstein's close-drawn lines of morphological tissue classification based on ontogeny were of little value, a new basis for anatomical description and classification was sought. This basis was found in function by Julius von Sachs (1832–1897), who made the first physiological classification. Epidermal, fibrovascular, and fundamental tissues derived from a uniform meristem were suggested by him as the basic types. The epidermal tissues included all outer protective tissues; the fibrovascular, all actually conducting cells; the fundamental was a catch-all for whatever did not fall into the other two groups, such as medullary rays, the pith, the cortex. This classification met with opposition on the part of anatomists, for whom De Bary expressed the general feeling in his views that, though Hanstein's system could not be rigidly applied, only a classification based on development could be most satisfactory and most useful.

The physiological viewpoint of anatomy, thus begun, became more prominent in the work of Simon Schwendener (1829–1919). The classification of tissues on a physiological basis was extended by Schwendener's researches and has reached high development in the work of Gottlieb Haberlandt, now professor of plant physiology at the University of Berlin. The latter has worked out in detail a complete physiological plant anatomy, presented in his textbook, "Physiologische Pflanzenanatomie," which has appeared in several editions from 1884 to 1918. In this book the physiological viewpoint dominates all structural description; purely morphological classifications or arrangements are disregarded. Tissues are grouped according to function, constituting systems called dermal, absorbing, conducting, storage, aërating, sensory, etc. In such classification a tissue is not necessarily structurally continuous, the cells forming a given tissue being perhaps distributed through various parts of the plant body, as, for example, in the case of conducting tissue, where, in the morphologist's "xylem," only the vessels, tracheids, and

parenchyma form the conducting tissue; fibers and fiber tracheids belong to the mechanical system. Thus, in many kinds of wood, such as that of *Acer*, what to the morphologist is xylem contains scattered through it only a rather small proportion of the physiologist's xylem. In similar ways terms are used in senses wholly physiological except for occasional cases when the basis is said to be "topographical." Whether physiological anatomists desire to supplant morphological conceptions may perhaps be questioned; they have, however, developed the structural material in such a way that it is useful chiefly to the physiologist. In the establishment of these conceptions, a considerable element of confusion has been added to the already confused state of anatomical terminology, since new terms have not been coined to any extent by physiologists, but those already in use have been applied in senses more or less different from their original meanings. To the physiologist the phylogenetic origin of a tissue or the fundamental nature of a cell type is of no direct importance. Physiological anatomy is, therefore, of value to the physiologist rather than to the anatomist; Haberlandt's text, however, because of the thoroughness with which the ground is covered, is generally useful to all students who are able to "translate" the terminology.

In the work of Eduard Strasburger (1844-1912), experimental physiology is combined with morphology in extensive cytological and anatomical studies. Though Strasburger is perhaps known best for his cytological contributions, his "Histologische Beiträge" contain the results of extensive and important anatomical researches. These relate chiefly to the conducting system of all plant groups, but especially of gymnosperms where his studies are very complete. In these papers he puts forward the idea of two distinct tissue systems, the cortical, or assimilating, and the conducting, or stelar.

The Stelar Theory.—The lack of a comprehensive presentation of the structure of the plant body as a whole, which is the outstanding weakness of De Bary's book, was supplied by the French botanist, Philippe Edouard Leon van Tieghem (1839-1914—Fig. 146) and his students, in the establishment of the stelar theory. Van Tieghem in 1870, before

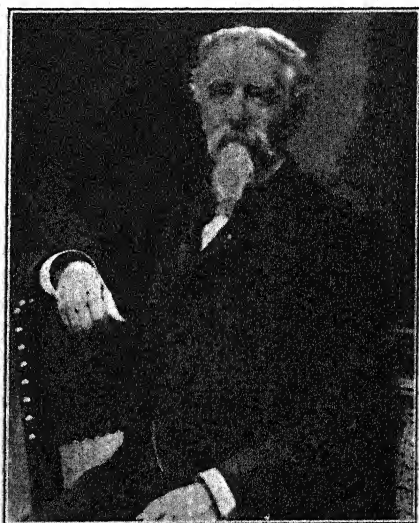


FIG. 146.—Philippe Van Tieghem (1839-1914).

the appearance of De Bary's text, had already begun the presentation of a new way of looking at the general structure of the plant axis. In the following years he extended his observations, and elaborated his theory that both root and stem are fundamentally alike in structure, each possessing a distinctly limited central core, which he termed the stele, surrounded by a protective layer, the cortex. Van Tieghem's stele is limited externally by the pericycle, and his cortex includes the epidermis on the outside and the endodermis on the inside. The stele, both in roots and in stems, does not consist of vascular tissues alone, but also of "conjunctive tissue," in which the conducting tissues lie: in the roots, pericycle, pith, and the tissues between the primary strands; in the stem, pericycle, pith, and medullary rays. Van Tieghem pointed out that the stele was not so distinct in the stem as in the root, owing to the disturbance in the tissues caused by leaf traces, to frequent absence of the endodermis, and to variation in the pericycle.

Later, van Tieghem and his pupils elaborated the stelar theory, extending it to cover, in its modifications, all types of axes, and giving names to the varieties of stelar structure. They spoke of the type where xylem and phloem are arranged in a simple hollow cylinder as a monostele. Where such a stele is broken up radially by the invasion of the pericycle and endodermis, so that the cortex becomes continuous with the pith, and the segments of the cylinder are surrounded by the pericycle and endodermis, the stele, as such, is not obvious, except in outline; hence, an astelic condition is present. In astely, there is thus the appearance of a number of isolated steles in a parenchymatous matrix. Where such isolated strands become fused laterally, the endodermis and pericycle being lost between them, but united to form a complete ring on their inner side—as, for example, in certain species of *Equisetum*—a condition of fusion or gamostely exists. Where, in ontogeny, the monostele of the young plant forks, as the axis elongates, to form two or more strands similar to the first-formed stele, a polystelic, or dialystelic, condition is developed. Such polystely occurs in some angiosperms and in many ferns. Ultimately, the term "polystely" was, however, applied by van Tieghem to both the gamostelic and the dialystelic conditions. Strasburger supported van Tieghem in the chief features of the latter's stelar theory, but proposed the term schizostely to replace van Tieghem's astely.

With the establishment of the stelar theory a big step was thus made in a comparatively brief period toward the understanding of the fundamental grosser structure of the axis. That this step was fundamentally sound has been shown by the subsequent study of many students.

Van Tieghem, in his attempt to explain the variations of steles, adopted the basis of comparative morphology and phylogeny, the only basis on which a satisfactory explanation could be made. Chiefly in respect to the unity of all stelar forms as modifications of a single

type, and as to the relations of leaf traces to the formation of broken steles, did van Tieghem fall short of a complete understanding of the theory. These conceptions, which are of the greatest importance to the stelar theory, were supplied in 1897 by Edward Charles Jeffrey, now professor at Harvard University. Professor Jeffrey, from an extensive study of all groups of vascular plants, and especially of the development of the stele in young plants, drew generalized conclusions concerning the nature of steles. Though agreeing in the main with van Tieghem concerning the nature of the stele he showed that the French anatomist's types had after all little morphological foundation. There are, he said, but two types of central cylinder, the siphonostele and the protostele; and these are fundamentally the same, since the former has clearly been derived from the latter. The protostele is a solid rod of vascular tissue in which a core of xylem is surrounded by phloem, and this by a pericycle; the siphonostele is similar to the protostele but is tubular, possessing a central pith, which Jeffrey claims arose phylogenetically as an invasion of the stele by the cortex. Thus the siphonostele is merely a modified protostele. Van Tieghem's types are but modifications of the siphonostele, the polystele not representing a "bifurcated epicotyledonary stele," nor the astelic condition the splitting of a monostele into definite bundles. The presence of breaks in the continuity of the vascular cylinder, which are related to the exit of leaf and branch traces and hence known as foliar and ramular gaps, is responsible for the apparent formation of distinct types of stele. Where the gaps are small, they may readily be overlooked, but where large, and when they overlap in longitudinal extent, the cylinder apparently consists only of isolated bundles. It is, however, a tubular network, perforated by extensive gaps. In the ferns, gymnosperms, and angiosperms, both leaf and branch gaps are always present, a condition Jeffrey termed "phyllosiphonic," in the horsetails, clubmosses, and related plants, only branch gaps occur, the cladophonic condition.

Jeffrey claims that the pith is extrastelar in morphological nature, representing cortical tissue which has invaded the stele in its phylogenetic specialization. With the invasion of the stele by cortex, the phloem, pericycle, and endodermis also entered the core of xylem. Thus the primitive type of siphonostele possesses internal phloem, pericycle, and endodermis. With greater specialization, these become degenerate and may disappear, there remaining only a perimedullary zone to represent these tissues morphologically. The importance of Jeffrey's conclusions was immediately recognized; a satisfactory understanding of varied stelar structure could now be had, and the great value of this to all anatomy was evident. It explained, for example, for comparative and physiological anatomy the presence of vestigial internal phloem and endodermis; it brought out characters of the greatest importance in the phylogenetic relations of the large groups of vascular plants. Through

the presence or absence of leaf gaps, together with other characters, Jeffrey made a new arrangement of the larger groups of vascular plants. The two groups thus formed, the Pteropsida and Lycopsida, have largely been accepted as natural, and their establishment has done much to aid in the determination of the phylogenetic relationships of the larger groups of vascular plants.

As to the method by which the pith arose in the protostele, a controversy arose between Jeffrey and certain English anatomists. Jeffrey's opponents claim that, at least in some groups, especially the eusporangiate ferns, the pith is not extrastelar, that is, cortical, in nature, but represents unspecialized xylem; that is, the pith is strictly stelar. The development of a pith in this way has been said to be by expansion, an unfortunate term, since it implies enlargement of the stele, a feature which does not necessarily exist. The discussion of the expansion and the invasion theories still continues sporadically, though it seems to be universally granted that in most plants the pith is doubtless cortical in nature. The establishment of the stelar theory has supplied a basis for an understanding of the structure of the plant body such as was not possible before. This alone has brought the vascular skeleton to the front as of much importance in the study of phylogeny.

Anatomy in Taxonomy.—The attention of anatomists was first called to features of internal structure as of importance in classification in the days of von Mohl; after the establishment of the theory of descent, the value of internal morphology in classification became increasingly evident. De Bary became one of the most prominent exponents of the anatomical method in taxonomy. The movement in this direction spread most rapidly in Germany as concerned living plants, and in England for fossil forms. The influence of the tendency to add anatomical features to the commonly used external morphological structure in taxonomy is evident in such important works as Engler and Prantl's "Die natürlichen Pflanzenfamilien" and Solereder's "Comparative Anatomy of the Dicotyledons."

Present-day Anatomy.—At the end of the nineteenth and the beginning of the twentieth century anatomical research turned definitely to the aid of taxonomists and morphologists in the solution of problems of natural relationship. Paleobotany, as a strong ally in this phylogenetic research, continued to stimulate progress in knowledge of anatomy through its constantly increased demand upon anatomy as a tool in the unraveling of the identity of fossil plants and of their relation to living forms.

During the past thirty-five years many prominent anatomists in England, France, and America have given their attention in greater or less part to problems of paleobotany. Perhaps the larger number of anatomists in these countries have, however, been more closely associated

with the anatomical aspects of comparative morphology. The many studies of the vascular anatomy of the pteridophytes made in the first years of the century and carried on largely in relation to stelar theories, and to questions of the validity of classification in this group, were doubtless to a large extent responsible for the increased recognition of the importance of the vascular skeleton as indicating natural relationships. The determination of this importance may be said to be without doubt the great contribution of anatomy to the solution of the problems of phylogeny.

Because of this recognition of the value of the study of the vascular skeleton, anatomical research in America has centered about the stele and its vascular appendages, especially about the phylogenetic value of these important structures in their various modifications. In England also the viewpoint of phylogeny dominates the studies of prominent anatomists; in France, comparative morphology perhaps stands much as it has throughout recent years in that country, largely above other aspects of anatomy; in Germany, physiological anatomy, under the influence of Professor Haberlandt, chiefly holds sway in the anatomical field.

To evaluate satisfactorily the anatomical research of the present time is clearly impossible. Moreover, even an outline of the contributions of the numerous individual investigators of today and of recent years is out of place in a brief and introductory sketch of this type. Therefore no attempt is here made to describe in detail the present situation in anatomy. Though the workers are many, the field is a very large one, the anatomy of the angiosperms being still largely unknown, and the opportunities for important contributions, both to descriptive and to comparative anatomy, are many.

Although at the present time the more "popular" fields of botanical research—physiology, cytology, and genetics—far surpass anatomy in commanding the interest of students, these fields are constantly demanding more and more complete information concerning structure. The requirements of these fields, together with those of applied botany, such as pathology and horticulture, must be met by anatomists; and all these fields must doubtless rely in the future in increased measure upon the information secured by morphology and anatomy.

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